Ann. Natal Mus. Vol. 32 Pages 221–277 Pietermaritzburg October, 1991

Amphibia Zambesiaca 5. Zoogeography

by

J. C. Poynton[1] and D. G. Broadley[2]

ABSTRACT

The Zambesiaca area includes Botswana, Caprivi (Namibia), Zambia, Malaŵi, Mozambique and Zimbabwe. One apodan and 113 anuran species are currently recognised in the area. The area does not constitute a distinctive zoogeographical unit; agglomerative classification suggests it includes a section of an East African lowland fauna, an adjoining upland (part Afromontane) complex, west of which is a mosaic of species clusters on the interior plateaux. This classification is tested by means of a transect. Virtually the whole area is included in the ranges of five species, while 24 species and subspecies are endemic, mostly localised on the eastern uplands. These uplands have the greatest species diversity (total of 79 species and subspecies), receiving subtraction margins of the eastern and the western plains faunas in addition to the upland complex. The eastern lowland carries the largest homogeneous fauna of 38 species (including 2 subspecies). Relationships between species ranges and environmental patterning show complexities which at present are for the most part not clearly identified and understood; temperature appears to be of particular underlying importance.

INTRODUCTION: ZOOGEOGRAPHICAL APPROACH AND METHOD

Very few amphibian species include the whole of the Zambesiaca area within their range. A primary task of a zoogeographical study of the area is therefore to attempt to identify any discrete clusterings of species and subspecies ranges; as Hengeveld (1990: 56) has recently argued at length, 'classification remains the first stage in the description and analysis of biogeographical patterns'. The detection, description and analysis of range clusters forms the major part of present study. Beyond this lies the objective of identifying the network of factors that have shaped the present distribution patterns. This requires an understanding of the spatial behaviour of taxa in response to environmental variability (Hengeveld 1990: 72), and a knowledge of environmental history. Many conceptual and practical difficulties beset this task, which are considered in this study to the extent allowed by the currently limited amount of biological and environmental information. Another task is the plotting of locality records published in earlier parts of this series (Poynton & Broadley 1985*a* 1985*b* 1987 1988), to assist zoogeographical analysis within a broader context of distribution patterns over Africa. These records, together with more recent records listed in an appendix and in Channing (1989), are presented on maps which also show most published locality records from surrounding territories, to indicate ranges beyond the Zambesiaca area. The maps are not however intended to be exhaustive regarding extralimital records. Locality records for the Transvaal, many of them new, have been compiled by Jacobsen (1990); some of the records that are particularly relevant to the present study have been included in the accompanying maps.

---

[1] Department of Biology, University of Natal, King George V Avenue, Durban 4001, South Africa.
[2] Department of Herpetology, Natural History Museum of Zimbabwe, P.O. Box 240, Bulawayo, Zimbabwe.

The literature on African plant and animal distribution has tended to give limited attention to biogeographical principles, approaches and methods (Poynton 1986). One result is that the treatments of different authors allow only uncertain comparisons. At the outset of this study, therefore, some discussion of approaches and methods is appropriate.

The present study is range-based, the known ranges of species being regarded as the primary data for biogeographical classification. This contrasts with habitat-based or district-based treatments, where distribution is analysed and presented on the basis of species lists drawn up according to preconceived divisions, usually based on habitat types or some set of climatic factors (Poynton 1964*a* 1986). The use of presumed causative factors as classification criteria in biogeography tends to lead to circularity, preventing, as Hengeveld (1990) has argued, the use of the units so distinguished either in their own terms or in other terms. District-based treatment is evident in perhaps the majority of older studies on African animal distribution. It is well illustrated by Loveridge's 'zoogeography' of the East African amphibian fauna (Loveridge 1937). Loveridge attempted 'to assign the herpetofauna to life zones' (1937: 486). He cited similar work by Parker, and was mildly critical of Parker's (1932) departure from a district-based approach in his assignation of 'ubiquitous, widespread species that occur in several habitats' to a 'separate group'—a procedure which is essentially range-based.

Loveridge nevertheless drew up a list of 'virile, ubiquitous types' before grouping species according to the nine 'life zones' which he recognised. As is common in the district-based approach, he did not specify the basis for his selection of these zones. Examination shows them to be defined by a combination of limnology, vegetation types and altitude. The culmination of Loveridge's analysis was the assignation of 'every species . . . to its correct ecological habitat' (1937: 504–505). This may seem to have little zoogeographical content in a strict sense; but Loveridge did, in his list of conclusions, give much attention to the likelihood of currently disjunct sylvicolous taxa having had past connections both between East and West Africa, and between areas within East Africa. These conclusions lie within the ambit of historical zoogeography.

Poynton (1962) noted that other zoogeographical conclusions could be drawn from Loveridge's lists, notably that the great majority of anuran species listed as occurring below 1 000 ft (305 m) are widely distributed, in contrast to species listed in the highest zone, which mostly have restricted ranges. This feature, namely of the East African lowlands being populated almost entirely by species that are widely distributed, was picked up in Schiøtz's (1976) study of the distribution of East African treefrogs. Schiøtz recognised several 'distributional patterns'. Only one of these is explicitly range-based, in that its member species are 'distributed throughout the area' (1976: 335). This parallels the treatment of the 'ubiquitous, widespread species' by Parker (1932) and by Loveridge (1937). Schiøtz further recognised an 'East African lowland fauna', occupying the coastal savannas from Kenya to South Africa, and two savanna 'elements' distributed north and south of the Congo forest block. In addition, he recognised a forest complex, composed of one 'element' that was regarded as an eastward extension of the Congo forest block fauna; and another fauna in the coastal area, divided into a 'farmbush element' distributed over the same area as the East African lowland savanna fauna, and a 'highforest element' restricted to forested mountains.

Schiøtz (1975) had published maps plotting locality records of nearly all the East African treefrog species, but it is not clear from his zoogeographical paper (1976) whether his 'faunas' and 'elements' were based on an agglomerative classification of the species ranges themselves, or whether the species were sorted and grouped according to previously conceived biochoria, to which amphibian distribution itself may have been a contributory factor. Uncertainty regarding underlying principles is also suggested by the statement that some of the distribution patterns may be 'ecological rather than zoogeographical separations' (1976: 335).

Yet there are important zoogeographical conclusions obtained in Schiøtz's study, notably his recognition of an 'East African lowland fauna', and of a more westerly savanna 'element' which is 'distributed south of the great forest in Angola and southern Zaïre and often extending into Zambia and Tanzania' (1976: 336). These conclusions certainly allow comparisons to be made between Schiøtz's and the present study.

In range-based studies such as the present one, the quality of the data naturally rests on the quantity of the available locality records. The fewer the records, particularly in the region of species margins, the more poorly definable will be the known species ranges—to the extent that ranges are clearly definable at all: especially in regions of only gradual environmental change, margins appear to be naturally 'fuzzy' in a sense discussed by Sattler (1986). Moreover, in practice, an arbitrary distinction may have to be drawn between a margin (or boundary) as a limit to 'normal existence', or as a limit to random movement (eg. McCoy, Bell & Walters 1986). To assist in the evaluation of the quality of the range data, a map showing the distribution of collecting is provided (Map 1). Every quarter-degree square from which one or more specimens have been collected has been marked. Collecting intensity (or success) between Beira and Chinhoyi is shown in more detail in Table 3. It is evident from Map 1 and Table 3 that collecting has been essentially unsystematic, dependent mainly upon where collectors have resided and where their favoured collecting sites and routes to them have been, rather than upon some planned filling-in of sampling grids. Large tracts of the Zambesiaca area are uncollected, or are very incompletely sampled.

As a result, it seems premature to investigate mechanical methods of range classification over the whole Zambesiaca area. The most commonly favoured mechanical method is to partition the study area by means of a grid, and score each quadrat in some way (eg. Alexander 1989, Owen 1989, Crowe 1990). The usefulness of classifications and ordinations obtained by this method depends primarily on the grid size: the finer the grid, the finer the resolution of the patterning; yet the more dependent the method becomes on close and uniform sampling across the study area. A quarter-degree grid has been used for plotting distributions in this study. In the latitude of the Zambesiaca area, the grid-quadrat size is about 729 km^2 (27 km on a side). For the purposes of classification and ordination over a large area, most authors settle for a larger grid size; Crowe

(1990), for example, used a grid-quadrat size of 48 400 km^2 (220 km on a side) in an analysis of patterns of amphibian distribution. Yet we consider that even a quarter-degree grid allows only a barely acceptable resolution of patterning in regions of abrupt environmental change, as on the eastern highlands, where analysis is in fact most needed. On the other hand, a quarter-degree grid contains too many unsampled squares, both regarding amphibian distribution and environmental (notably climatic) patterning, to allow mechanical methods to function except in a particularly well-collected region, such as the Beira–Chinhoyi transect to be described below.

In this study, therefore, the general procedure for identifying common distribution patterns is the same as that adopted in an earlier zoogeographical study of the southern African amphibian fauna (Poynton 1964*a*), which attempted an agglomerative classification of ranges (as far as they can be defined) by direct inspection of the available locality data plotted on quarter-degree grid maps. In the present study, species and subspecies ranges were copied onto separate overhead transparencies, which allowed easier sorting and grouping. No particular ranges were given preferential weighting, such as ranges of species endemic to the Zambesiaca area, since this area is arbitrarily chosen.

The results of the range grouping are presented in the following section. As in the previous study, 'this grouping is not done in the belief that an absolutely rigid classification is possible' (Poynton 1964*a*: 222). The same view has recently been strongly expressed by Hengeveld (1990: 49), namely 'that classifications are heuristic and that they should be used only as starting points for further research, rather than descriptions of objective, natural units, being ends in themselves'. As Hengeveld points out (1990: 63), 'Classifications are not right or wrong, only useful or not.' This is a result of the inductive basis of classification. Being inductive generalizations, they are constantly open to revision: as Sattler (1986: 18) has put it, 'inductive generalization does not lead to statements whose truth can be asserted.' In this Popperian vein, biogeographical classifications can be seen as theories or hypotheses; in which case the matter of *how* a classification is arrived at is unimportant (cf Popper 1972), whether it be by mechanical, computer-assisted techniques or by direct inspection. All that matters is that the classification is open to testing. Later in this paper, the present classification will be tested by examining a transect along the best collected route in the area, namely the route from Beira through Mutare and Harare to Chinhoyi (formerly Sinoia).

In the school of biogeographical thinking which sees phylogeny as an essential input into biogeography (eg. Humphries, Ladiges, Roos & Zandee 1988), the assessment of phylogenetic relationships becomes a major concern in the biogeographical classification. Among African amphibians, phylogenetic assessment at the species level has been inhibited by a lack of clear-cut external characters in the adult stage, and by uncertainties in assigning polarity to those character states that can be defined. Tadpoles may be more promising a source of accessible structures that allow phylogenetic analysis, and it is to be hoped that the present study will encourage more work in this direction. It will be evident from the following pages that the present situation is far from satisfactory.

TAXONOMIC ADJUSTMENTS

Since the publication of Part 3 (Ranidae) in this series (Poynton & Broadley 1985*b*), Perret (1987) has shown that the name *Ptychadena cotti* is a junior synonym of *P. schillukorum* (Werner 1907). A specimen from Eastern Caprivi (Namibia), identified by Channing (1989) as *P. cotti* (CAS 160535), does not appear to belong to this species. In external appearance and sonagraphed call (Channing 1989 Fig. 1A), it most closely resembles *P. mossambica*; the sonagram differs markedly from the sonagram of (presumably) *P. schillukorum* published (as *P. floweri*) by van den Elzen & Kreulen (1979) from the Serengeti National Park. Western populations of this species were said by Poynton & Broadley (1985*b*) to show unusual features, and renewed taxonomic investigation of western material seems to be called for. Channing's (1989) Eastern Caprivi record of *P. upembae* is based on misidentification of *P. guibei*, judging from CAS 160624. It was noted in Poynton & Broadley (1985*b*) that the paravertebral folds tend to be continuous in material from Botswana and western Zambia; this indeed appears to be the rule in material from about Victoria Falls westwards (but not Upemban material). Renewed taxonomic investigation of material, including that of *P. chrysogaster* (of which *guibei* was initially proposed as a subspecies) is needed, particularly in view of the possibly anomalous range of *guibei* as at present understood (see below). The key to *Ptychadena* in Poynton & Broadley (1985*b*) may be altered in the following way to take variation in *guibei* into account:

14 Less than 3½ phalanges of fourth toe free of web 15
— At least 3½ phalanges of fourth toe free .... **keilingi** (p. 154)
15 Cross-banding present on upper surface of tibia .... **upembae** (p. 150)
— Upper surface of tibia with uniform coloration, not cross-banded .... **guibei** (p. 154)

Note should be taken of the caution given in the original key that it is not possible to make reliable identifications on the basis of the keys alone. The species diagnoses and descriptions should be studied, preferably in conjunction with comparative material.

Namibian material referred to *Phrynobatrachus stewartae* by Channing (1989) attains a size of 20 mm and is shown by dissection to be immature. Sexual maturity should be evident in *P. stewartae* of this size, and also by *P. mababiensis*, which this material approaches in the limited webbing, being incised to below the level of the distal tubercles of the third and fifth toes. The material is here considered to be juvenile *P. natalensis*, but with some uncertainty on account of the limited webbing. Further study of Namibian material is clearly needed. The locality records provided by Channing (1989) are included in the accompanying maps, with the changes *Bufo vertebralis* = *Bufo f. fenoulheti* and *Hyperolius aposematicus* = *Hyperolius marmoratus angolensis* (Channing pers. comm.).

A 36 mm *Bufo* recently collected from Zambezi Rapids, northwestern Zambia (NMZB 10630), broadly agrees with *fuliginatus* but it would not key out to this species in Poynton & Broadley (1988) on account of possessing a row of light-tipped glands under the forearm. Re-examination of material in the British

Museum (N.H.) suggests that this feature is present at least in juvenile specimens. The character of a darkly pigmented ventral skin may be inserted in the key to separate *fuliginatus* from *B. garmani, kisoloensis* and *gutturalis* (while bearing in mind the inadequacies of keys).

Of three *Breviceps* specimens recently collected from northwestern Zambia (NMZB 10534–5, 10652), two show slight lateral darkening, a feature developed to varying degrees in Angolan material (Poynton & Broadley 1985*a*). In the Zambian specimens, the outer finger just reaches the distal tubercle of the third finger, which is more like typical *B. mossambicus* than like some of the Angolan material. On their own, the Zambian specimens are not readily separable from *B. mossambicus*, but they should be taken into account in a much-needed study of complexities in Angolan *Breviceps*.

RANGE CLUSTERING IN THE ZAMBESIACA AREA

According to the taxonomic analysis carried out in this study, one apodan and 113 anuran species are known to occur in the Zambesiaca area. Eight species have two or more subspecies in the area (15 subspecies in the case of *Hyperolius marmoratus*), giving a total of 136 forms. The ranges of most of these taxa extend beyond the area, and the broadest overall pattern is a turnover of ranges from east to northwest. Within this overall pattern, range clusters may be fairly readily detected. Those identified in this study are named according to the common geographical area or 'centre' of each cluster, from which a gradient of declining species diversity, or subtraction margin, is perceived to spread. This perception is rendered uncertain particularly in areas where range limits are not known owing to a lack of collecting. Where records are missing, the use of 'biological judgement' is reasonable (eg. McCoy, Bell & Walters 1986), and hopefully encourages further sampling.

In most cluster groups, the forms are listed in a sequence starting with the smallest range present in the Zambesiaca area (but not necessarily the smallest range in the continent as a whole) to the most widespread. Each group is given a code, allowing ready assignment of every species or subspecies to its group in the following discussion. Species or subspecies endemic to the Zambesiaca area (totalling 24 taxa) are indicated by **end**.

EA—East African lowland

At least a substantial portion of the range includes the coastal lowlands of East Africa (Mozambique, Tanzania and Kenya below 300 m).

This group, analysed by Poynton (1990), includes some very widespread species, some with western limits in Angola. It could be held that the classification of such species as 'East African lowland' lays too much emphasis on one portion only of their total range. If this view is held, then about the last five species listed here could be placed in a category under some such designation as Parker's (1932) 'ubiquitous, widespread'. This selection would be arbitrary. Nevertheless, there is some arbitrariness about separating this group from the most widespread members of the Northwestern Group (NW), as noted under that group. The apparently scattered distribution of *Ptychadena guibei* (Map 27) on the eastern lowlands could disqualify the species from belonging to this group; this is another case showing some arbitrariness in separating the eastern lowland group from the Northwestern Group (NW). *Schismaderma carens* (Map 57) also shows scattered distribution on the eastern lowlands, which might be associated with a lack of deepwater breeding sites in the region.

Sequence from smaller to greater extension westwards: *Hyperolius parkeri*, *Ptychadena schillukorum*, *Hylarana galamensis*, *Hyperolius mitchelli*, *Leptopelis broadleyi*, *Afrixalus fornasinii*, *Leptopelis flavomaculatus*, *Hyperolius argus*, *Hyperolius tuberilinguis*, *Phrynobatrachus acridoides*, *Leptopelis mossambicus*, *Hyperolius pusillus*, *Kassina maculata*, *Afrixalus crotalus* (**end**), *Hyperolius marmoratus taeniatus*, *Arthroleptis stenodactylus*, (?) *Schismaderma carens*, (?) *Ptychadena guibei*, *Breviceps mossambicus*, *Hemisus marmoratus*, *Pyxicephalus adspersus edulis*, *Ptychadena anchietae*, *Ptychadena mossambica*, *Xenopus muelleri*, *Chiromantis xerampelina*, *Ptychadena oxyrhynchus*, *Hyperolius nasutus*, *Ptychadena mascareniensis*, *Phrynobatrachus mababiensis*, *Hildebrandtia o. ornata*, *Kassina senegalensis*, *Bufo garmani*, *Phrynomerus bifasciatus*, *Bufo gutturalis*, *Bufo maculatus*.

The following may also be included in this group, although their taxonomy or known distribution is surrounded by particular uncertainty: *Bufo lindneri*, *Pyxicephalus adspersus angusticeps* (**end**), *Tomopterna krugerensis*, *Afrixalus delicatus*.

MZ—Malaŵi (+ adjacent Mozambique highland) and eastern Zambia

Sequence roughly from larger to smaller range; the ranges outside the Zambesiaca area tend to be relatively small in the members of this group, usually including only the southwestern Tanzanian highlands.

Afrixalus sp. and *Afrixalus brachycnemis* (Map 41) are included in this group even though, according to current taxonomy, their distribution includes both Malaŵi and the lowlands of northern Tanzania and Kenya (eg. Schiøtz 1976, figs 85, 86). The current taxonomic picture requires clarification, however (Poynton & Broadley 1987), and consequently only the distribution in Malaŵi is here taken into account. The distribution of *Hyperolius puncticulatus* (Map 46) is similar to these *Afrixalus* species, although in this case the taxonomic situation seems more clear (Poynton & Broadley 1987). This species shows a tendency to be associated with forest; it is included in this MZ group on account of its range at least within the Zambesiaca area being typical of the group. The wide-ranging *Arthroleptis xenodactyloides* (Map 10) is included in this group even though it occurs in lowland forest around Beira; its occurrence there is presumably allowed by the relatively dense treecover present (cf Prigogine 1987). It is commonly found at higher elevations, where it can occur outside the shelter of forest. (n) = northern, and (s) = southern restriction in Malaŵi.

Arthroleptis xenodactyloides, *Afrixalus* sp, *Afrixalus brachycnemis*, *Hyperolius puncticulatus*, *Strongylopus fasciatus fuelleborni*, *Phrynobatrachus ukingensis*, *Hyperolius viridis*, *Hyperolius pictus* (n), *Hyperolius marmoratus nyassae* (n, **end**), *Arthroleptis reichei* (n), *Bufo kisoloensis* (n), *Bufo lonnbergi* (n), *Hyperolius quinquevittatus mertensi* (n, **end**), *Phrynobatrachus stewartae* (n, **end**), *Hyperolius spinigularis* (s), *Scolecomorphus kirkii* (s), *Hyperolius marmoratus albofasciatus* (s, **end**) *Nothophryne broadleyi* (s, **end**), *Rana j. johnstoni* (s, **end**), *Ptychadena broadleyi* (s, **end**), *Leptopelis* sp (s, **end**), *Arthroleptis francei* (s, **end**).

EZ—Eastern Zimbabwe (+ adjacent Mozambique highland)

As in the MZ group, forms tend to be restricted to the northern or the southern region of the Zimbabwean highlands, and are designated (n) or (s). This group is examined as Set 4 in Tables 2 and 5 and the accompanying text.

Strongylopus grayii rhodesianus (**end**), *Rana johnstoni inyangae* (n, **end**), *Probreviceps rhodesianus* (n, **end**), *Bufo gariepensis inyangae* (n, **end**), *Bufo fenoulheti grindleyi* (s, **end**), *Hyperolius marmoratus swynnertoni* (s, **end**), *Arthroleptis troglodytes* (s, **end**), *Stephopaedes anotis* (s, **end**).

NW—Northwestern

Centre in the northwestern half of the area (extending into Angola), southern and eastern margin extending into mainly upland regions. While a clear division cannot be made, there is a tendency for the margin to separate into a western set of ranges extending into Botswana, and a set with more easterly extensions (sometimes disjunct) into the eastern uplands. The most widespread species (the last seven listed) extend to South Africa (where populations may be disjunct) and the east coast, but they are largely absent from the coastal lowlands within the Tropics. Noteworthy are the eastern edges of the ranges of *Rana angolensis* and *Phrynobatrachus natalensis* (Maps 15 & 31), which are very similar. *Tomopterna cryptotis* (Map 12) has a few more records from the lowlands, but the general absence of these three species from coastal lowland in tropical and equatorial regions excludes them (albeit not decisively) from the 'East African lowland' group, into which they were placed with reservations by Poynton (1964*a*). Their occurrence inland of Beira is evidently encouraged by the presence there of fixed vegetated river banks, a favoured habitat particularly of *Rana angolensis* that is not normally found on the Mozambique Plain.

Sequence broadly from smaller to larger range: *Ptychadena bunoderma*, *Ptychadena keilingi*, *Leptopelis cynnamomeus*, *Hyperolius platyceps major*, *Hyperolius marmoratus alborufus*, *Hyperolius marmoratus angolensis*, *Ptychadena ansorgii*, *Hylarana lemairei*, *Hyperolius bocagei*, *Kassina kuvangensis*, *Ptychadena grandisonae*, *Arthroleptis xenochirus*, *Afrixalus wittei*, *Hemisus guineensis microps*, *Phrynomerus affinis*, *Bufo lemairii*, *Ptychadena subpunctata*, *Xenopus laevis petersii*, *Tomopterna tuberculosa*, *Leptopelis parbocagii*, *Ptychadena upembae*, *Hyperolius q. quinquevittatus*, *Hylarana darlingi*, *Hyperolius benguellensis*, *Phrynobatrachus parvulus*, *Leptopelis bocagii*, *Ptychadena uzungwensis*, *Ptychadena taenioscelis*, *Ptychadena porosissima*, *Rana angolensis*, *Tomopterna cryptotis*, *Phrynobatrachus natalensis*.

NC—North-central

Centre in the northern part of the area between about 27° and 33°E, margin extending into Malaŵi and Zambia. There is a tendency for some of these forms to be associated with denser woodland or forest, notably *Bufo urunguensis*, *Bufo fuliginatus* and *Bufo melanopleura*.

Sequence from smaller to larger range: *Bufo urunguensis*, *Euphlyctis occipitalis*, *Hyperolius marmoratus argentovittis*, *Hyperolius marmoratus bitaeniatus*, *Hyperolius marmoratus rhodoscelis*, *Hemisus wittei*, *Bufo fuliginatus*, *Phrynobatrachus perpalmatus*, *Bufo melanopleura*, *Ptychadena obscura*, *Kassinula wittei*, *Phrynobatrachus rungwensis*, *Bufo taitanus*, *Hyperolius kivuensis*, *Breviceps poweri*.

C—Central

Centred in plateau areas north and south of the Zambezi.

Not arranged in biogeographical sequence. *Bufo beiranus* (**end**), *Bufo f. fenoulheti*, *Bufo kavangensis*, *Breviceps a. adspersus*, *Tomopterna marmorata*, *Hemisus guineensis broadleyi*, *Hyperolius kachalolae* (**end**), *Hyperolius marmoratus aposematicus* (**end**), *Hyperolius marmoratus broadleyi* (**end**), *Hyperolius marmoratus marginatus*, *Hyperolius marmoratus melanoleucus*, *Hyperolius marmoratus pyrrhodictyon* (**end**), *Hyperolius marmoratus rhodesianus* (**end**). *Hyperolius kachalolae* (Map 45) is included in this group although its range (as far as it is known) is unique. The range of *Bufo beiranus* (Map 55) is so anomalous as to suggest a need for taxonomic reassessment. Its occurrence in the Beira area is interpreted as representing a peripheral extension of a mainly central range. *Bufo kavangensis* (Map 54) could be assigned to a 'Kalahari Sand group' if more anurans showed this distribution. *Bufo f. fenoulheti* (Map 54) and *Breviceps adspersus* (Map 5) have extensive ranges south of the Limpopo, and could be considered to constitute a separate group, a possibility noted in Poynton (1964*a*: 227).

S—Southern

Distributed mainly south of the area, but with a margin extending northwards largely in the uplands, typically with disjunct ranges.

Sequence from smaller to larger ranges: *Afrixalus aureus*, *Cacosternum n. nanum*, *Tomopterna natalensis*, *Strongylopus f. fasciatus*, *Pyxicephalus a. adspersus*, *Cacosternum boettgeri*, *Xenopus l. laevis*.

DISCUSSION

Range clusters

It is evident from this analysis that the Zambesiaca area is not a distinctive biogeographical unit. Its eastern lowland is occupied by a section of an East African lowland fauna (EA; element 4 of Schiøtz) that extends from South Africa through to Kenya and Somalia (Poynton 1990). Bordering the lowland is a portion of the interrupted 'spine' of Africa which, in panbiogeographic terminology (eg. Croizat 1968), is distinguished by carrying a 'generalised track' extending along the uplands from South to East Africa (MZ & EZ). Members of the MZ and EZ groups would provide a starting point in the Zambesiaca area for investigating whether the idea of an 'Afromontane Region' (eg. White 1978) is applicable to amphibian distribution. Such an investigation is too wide-ranging to be included in the present study. The northern central and western regions of the Zambesiaca area are populated mainly by species that are widespread over the plateaux of the

South Equatorial Divide. These species are referable to Schiøtz's (1976) 'savanna element' distributed south of the Congo forest ('element 3'). The identification of two range clusters in this region (NW, NC) shows, however, that this 'element' is more complexly structured than is Schiøtz's 'element 4' occupying the eastern lowlands (EA). The subtraction margin of the northwestern group southwards is extensive and complex. Several species with ranges mainly south of the tropics (S) reach their northern limits in southern uplands of the Zambesiaca area.

The groups centred on the eastern upland chain (MZ, EZ) and the central plateau area (C) contain 83 per cent of the 24 species or subspecies whose known range is confined to the Zambesiaca area, coded **end** in the above lists. The East African lowland (EA) group is the only other cluster containing endemics. The majority of endemics (58%) occur on the upland spine of Africa which passes through the area, and they may be regarded as part of the upland 'track' extending from East to South Africa. Of these, the affinities of the *Strongylopus* endemic subspecies are evidently to the south, where the initial range (*sensu* Brundin 1981) of the genus is apparently located (Channing 1981, Poynton & Broadley 1985*b*); *Bufo gariepensis inyangae* also has affinities to the south (Poynton & Broadley 1988). The affinities of the *Rana johnstoni* subspecies and of *Arthroleptis troglodytes* have not been worked out; and inadequate analysis also obscures whether or not the only genus endemic to the Zambesiaca area, *Nothophryne*, has southern affinities, in the sense of being derived from 'Cacosternine' stock (Poynton 1964*a*) with a likely initial range in the south. The remaining upland spine endemics either appear to have closest affinities with other forms occurring in the Zambesiaca area, notably the *Hyperolius marmoratus* subspecies, or northwards with Tanzanian forms, notably *Probreviceps rhodesianus*, *Arthroleptis francei* (Poynton & Broadley 1985*a*) and *Stephopaedes anotis* (Poynton & Broadley 1988).

Within Malaŵi-eastern Zambia (MZ), seven species/subspecies are restricted to the northern part (ie. north of 13°S) and eight to the south, suggesting that the grouping 'MZ' may be too coarse. This could also be true of the eastern Zimbabwe-western Mozambique (EZ) group, with northern and southern subgroups. In the case of the MZ group, the first seven forms that are listed above have a wide distribution over the area, giving it the character of a single zoogeographical unit. Happold & Happold (1989) report that a high proportion of small mammal species have a similar wide distribution over the area. All the south-restricted forms are endemics except *Hyperolius spinigularis* and *Scolecomorphus kirkii*, which according to current taxonomy also have populations in Tanzania. The taxonomy needs closer investigation before much biogeographical weight can be placed on these recorded disjunctions: Schiøtz (1975) notes differences between Malaŵian *Hyperolius spinigularis* and the Tanzanian material which he referred to this species. The distribution pattern does nevertheless suggest the existence of relict populations; and this further suggests that the southern Malaŵian endemics are palaeoendemics rather than neoendemics, following the terminology of Myers & Giller (1988). A different situation is suggested by populations on the Nyika Plateau, which have only minor or uncertain taxonomic distinctiveness, namely *Hyperolius quinquevittatus mertensi* and populations of *Arthroleptis xenochirus*, *A. xenodactyloides* (Poynton & Broadley 1985*a*) and *Phrynobatrachus parvulus* (Poynton & Broadley 1985*b*). Current evolutionary activity is suggested by these cases, and in consequence *Hyperolius quinquevittatus mertensi*, which is surrounded by *H. q. quinquevittatus*, can be regarded as a neoendemic.

Schiøtz (1981) cited *Hyperolius spinigularis* as the only 'rain forest amphibian' common to Malaŵi and the eastern Tanzanian mountains. He was however in doubt about it being a 'true rain forest species', and indeed some doubt may be admitted as to whether the Tanzanian material is correctly identified. It appears that *Arthroleptis xenodactyloides*, which is associated with tree cover at least at lower elevations, occurs in the eastern Tanzanian mountains as well as the eastern Zambesiaca area (Poynton & Broadley 1985*a*), as does *Leptopelis flavomaculatus* (Schiøtz 1975). Schiøtz (1981) regarded *Probreviceps* as being endemic to the Eastern Tanzanian mountains, but *P. rhodesianus* occurs in Eastern Zimbabwe (Poynton & Broadley 1985*a*). The difference between the amphibian fauna of the eastern Zambesiacan and eastern Tanzanian mountains is nevertheless striking: six genera in Schiøtz's (1981) Tanzanian list do not occur in the Zambesiaca area.

Most endemics of eastern Zimbabwe-western Mozambique (EZ) appear to be relicts (*Strongylopus grayii rhodesianus*, *Rana johnstoni inyangae*, *Probreviceps rhodesianus*, *Bufo gariepensis inyangae*, *Stephopaedes anotis*), and consequently can be regarded as palaeoendemics. *Bufo fenoulheti grindleyi* and *Hyperolius marmoratus swynnertoni* appear to be local differentiations of widespread species, and could be regarded as neoendemics, while the status of *Arthroleptis troglodytes* in this regard is uncertain. Endemics of the central region (C) of the Zambesiaca area are *Hyperolius kachalolae*, *Bufo beiranus* and subspecies of the markedly vicariating *Hyperolius marmoratus*. As noted earlier, the ranges of the former two species are exceptional, and affinities have yet to be worked out. A need for more intensive work at this level of taxonomy was pointed out in the Introduction.

In broad terms, amphibian distribution in the Zambesiaca area can be seen as a complex mosaic of more or less clearly defined clusters, with an overlay of widespread species covering several or even all of these clusters. Distribution on the eastern lowland gives the impression of uniformity over vast distances, with abrupt transitions occurring in the eastern lowlands of South Africa and of Kenya/Somalia, and also in rising country to the west (Poynton 1990). Clusters to the west of the lowland were termed 'transitional units' by Poynton (1962, 1964*a*) on account of being situated in a perceived transition zone formed by the subtraction margins of an East African lowland fauna and a south-centred Cape fauna. The limited scale of the Zambesiaca area does not call for the use (or evaluation) of the term 'transitional' for these groupings, nor for a hierarchical arrangement of the clusters. The grouping in this study differs from the grouping of 'tropical transitional' amphibians in the southern African study (Poynton 1964*a*), on account of differing geographical scale and area. Hengeveld (1990: 48) goes so far as to assert that 'classifications of the same general area, but with dissimilar limits, will not be comparable.' Yet this appears to overstate the position, as will be discussed below (p. 238).

No strong bias is shown regarding the representation of particular genera in the clusters: each cluster has a wide sample of genera. In the 'central plateau' cluster

(C), which is not a well defined set, *Hyperolius* species and subspecies account for seven of the total of thirteen forms. It is not clear why *H. marmoratus* has undergone local differentiation in this plateau region, producing what are currently recognised to be six subspecies. It is indeed not clear why so many clusters are evident in the inland plains, where their presence might not be expected. A complex history is indicated, about which virtually nothing is currently known.

Distribution of diversity

As noted in the Introduction, the general paucity of locality records leads to a poor definition of known species ranges. This leads to imprecision in estimating the number of species/subspecies present in any particular area, and hence to imprecision in estimating species diversity—or species richness, both terms, following Brown (1988), being taken to reflect an estimate of species number in an area. The situation in the best collected region of the Zambesiaca area will be examined in the next section; by and large the available locality data do allow a reasonable estimate of the number of species and subspecies centred in each range cluster area, listed in the previous section. Table 1 shows the number of species and subspecies assigned to each 'centre', and also the total number, which includes forms known or considered likely to enter the area from some other centre.

TABLE 1

Species/subspecies diversity in Zambesiaca cluster areas. EA—East African lowland; MZ—Malaŵi & eastern Zambia; EZ—Eastern Zimbabwe & adjacent Mozambique; NW—Northwestern; NC—North-central; C—Central; S—Southern.

Range cluster area	No. forms assigned to each cluster centre	%	Total no. forms known or thought to be in cluster
EA	39	29	41
MZ	22	16	64
EZ	8	6	51
NW	32	23	59
NC	15	11	48
C	13	10	52
S	7	5	31

It may be seen from the table that although the East African lowlands (EA) cluster number is the greatest, Malaŵi and its immediate surrounds east and west carry a particularly high diversity. This is the result of the region lying in the margins of both the East African lowland fauna and the interior plateaux complex (elements 4 and 3 respectively of Schiøtz 1976), in addition to possessing the large number of species and subspecies scattered along the upland spine (MZ). The eastern highlands of Zimbabwe (EZ) is enriched in a similar manner, although the total number is smaller because there are fewer endemics, and the contribution from the interior plateaux is smaller, since the gain in some southern species is offset by the absence of many northern species. A total of 79 species and subspecies probably occurs in the upland spine region within the Zambesiaca area.

The attention of collectors and of biogeographers tends to favour mountainous regions rather than plains, usually on the grounds of the richness and peculiarities of montane floras and faunas. Afromontane areas are no exception. Fortunately, collecting on the eastern lowland and the Zambesiaca plateaux has been sufficient to show that these plains also possess great species richness, even though there are relatively few localised endemics; the interior plateaux also show considerable zoogeographical complexity, greater than might be expected. A more accurate knowledge of current range limits on these plains is needed.

Testing the classification by means of a transect

Biogeographical classifications, and the data on which they are based, may be investigated and tested by several methods. These methods have recently been reviewed by Hengeveld (1990). Use of a transect is one such method. The route from Beira (19°50'S:34°55'E) through Mutare and Harare to Chinhoyi (17°16'S:30°10'E) stands out as being particularly suitable for use as a transect, since it is better collected than any other route in the Zambesiaca area, and it traverses major features of the area, namely the eastern lowlands, eastern highlands and a substantial part of one of the interior plateaux.

As the route has not been systematically collected, it is necessary to represent the occurrence of species along it by means of grouping localities. The usual procedure of partitioning by means of a grid is followed here. The most convenient grid is the quarter-degree partitioning used in this study; but the route's north-easterly trend is a complication. The procedure adopted here is to treat the transect as lying between 18° and 19° S; but, in conformity with the north-to-south trending of the escarpment in this region, records are projected onto the transect from the blocks 17°–18° S × 30°–33° E (see Map 1), and 19°–20° S × 33°–35° E. The portion of the transect from 30° to 33° E then carries mainly upland localities, while the section 33° to 35° E carries mainly lowland localities.

The transect can be collapsed to a single east-west line, which is partitioned in quarter-degree intervals. Each interval, covering a distance of about 27 km, then 'reads off' a vertical column of eight quarter-degree squares. This allows a two-dimensional plotting of the recorded presence of each species in the transect zone, as shown in Table 2. The symbol + is used to indicate at least one positive record in the quarter-degree interval, while the symbol o indicates no record in intervals lying within the presumed range of the species or subspecies. The intervals are given the notation 30° a, b, c, d 31° a, b, c, d etc in later tables.

Estimation of the 'presumed range' of a taxon is not problematic in the case of the 16 taxa with records from Beira (or a nearby coastal station) through to stations west of Chinhoyi (indicated by > at the commencement of record lines in Table 2). These taxa are taken to range throughout the transect zone (Set 1 in Table 2). Other taxa (Set 2, Table 2) evidently fail to extend as far inland within the transect zone, although several species (indicated by * in Table 2) have a total range which includes the middle Zambezi to the west of the Zimbabwean plateau (see p. 241). The westerly 'known range limit' within the transect zone is taken to be the most westerly quarter-degree interval where a positive record exists. The 'known range limit' cannot be taken necessarily to be the actual limit, but it can

TABLE 2

Collecting records in quarter-degree intervals in the Chinhoyi—Beira transect, 30°–35 °E. + = positive record; O = no record within 'presumed range'; ! = isolated population; * = reappearing in the middle Zambezi Basin; > = continuing west of Chinhoyi. *Pyxicephalus adspersus edulis* and *P. a. angusticeps* are treated as a single taxon in view of recent taxonomic uncertainties (Poynton in press).

Phrynomerus b. bifasciatus	>OOO++O+O+O++OOO+++O+	
Breviceps mossambicus	>+OOO+O++OO+O++O+++OO	
Hemisus m. marmoratus	>++O++OO++O++OOOO++++	
Hemisus g. broadleyi	>OOO+OOOOOO+OOOOOO+O+	
Arthroleptis stenodactylus	>+OO++O+OOO++++++++++	
Tomopterna cryptotis	>+OO+OO+O+O+OOOOOOOO+	
Hildebrandtia o. ornata	>+OO++OO++O+OOOO++OO+	
Ptychadena oxyrhynchus	>+O+++++++O+++OO++O++	SET 1
Ptychadena anchietae	>++OO+O+++O++++O++O++	
Ptychadena mossambica	>+OO++OOOOO+OOOOO++++	
Phrynobatrachus mababiensis	>O++++O+++O++++++++++	
Chiromantis xerampelina	>+++OO+OO+++OOOO+++++	
Kassina senegalensis	>O+O++O+++O+++OO++++O	
Hyperolius nasutus	>+O+++O++OO+++O+O+OO+	
Bufo gutturalis	>++++++++O++++O++++O+	
Bufo maculatus	>++++++++++++++++++++	
Hylarana galamensis	+	
Ptychadena m. mascareniensis	* +	
Tomopterna krugerensis	* ++	
Afrixalus delicatus	++	
Hyperolius parkeri	+O	
Ptychadena schillukorum	+O+	
Leptopelis broadleyi	+O+O	
Hyperolius pusillus	+O++	
Bufo beiranus	* +++O	
Pyxicephalus a. edulis	* +++++	
Leptopelis mossambicus	+++++	
Hyperolius argus	++O++	SET 2
Hyperolius mitchelli	+OOOOO	
Hyperolius m. taeniatus	+O+++++	
Kassina maculata	+OO+OO++	
Ptychadena guibei	* +O+O+OO++	
Leptopelis flavomaculatus	+++O++O+O	
Arthroleptis xenodactyloides	+++OO++O++	
Phrynobatrachus acridoides	+++O++++++	
Afrixalus fornasinii	+++O+++O++	
Hyperolius tuberilinguis	+++O++++++	
Xenopus muelleri	* +O+O+O++O+++	
Afrixalus crotalus	+++++OO++OO+	
Hyperolius m. marginatus	>+	
Cacosternum boettgeri	>OOO++	
Tomopterna tuberculosa	>+OOO+O+	
Pyxicephalus a. adspersus	>OOO++OOO+	
Hyperolius benguellensis	>OOO++OOO+O+	
Bufo garmani	>+OO++OOO+O+	
Ptychadena porosissima	>OO+++O+O+O++	
Phrynobatrachus parvulus	>OO++++OOOO++	
Leptopelis bocagii	>O++++OOO+O++	SET 3
Tomopterna marmorata	>++O+OOOO++++	
Xenopus l. laevis	>O+O+++O++O+++ !	
Strongylopus f. fasciatus	+OO++O+OOO+++	
Ptychadena uzungwensis	>OOO++O+OOO+++	
Hyperolius m. broadleyi	>O+O++++++++++ !	
Bufo f. fenoulheti	>+OO++++++O++++	

TABLE 2 (cont.)

Hylarana darlingi	>O++++++++O+O+OOO+	
Schismaderma carens	>++O++OOOOO+OOOO++	
Breviceps a. adspersus	>+OO++O+++O++++O+++	
Phrynobatrachus natalensis	>++++++++O+++++++++	
Rana angolensis	>+++++++++++++++++O+	
Rana j. inyangae	+	
Bufo g. inyangae	+	
Bufo f. grindleyi	+	
Arthroleptis troglodytes	+	SET 4
Stephopaedes anotis	(!) +	
Probreviceps rhodesianus	++	
Hyperolius m. swynnertoni	+++	
Strongylopus g. rhodesianus	+++ !	

provisionally be taken to delimit the 'presumed range'. Yet other taxa (Set 3, Table 2) occur on the plateau at least as far west as Chinhoyi, but apparently fail to reach the coast or even the eastern lowlands; their easterly 'known range limit' is taken to be the most easterly quarter-degree interval containing a positive record. Two taxa have an apparently isolated component in some environmentally isolated location in Mozambique. Such isolates are indicated by the symbol ! in Table 2. Finally, some taxa (Set 4, Table 2) appear to have a restricted range within the transect zone. Their 'presumed range' is confined to the eastern highland ridge, but one has an isolated population in Mozambique (Gorongoza Mountain). *Stephopaedes anotis* has two known localised populations, the western population indicated by (!) because it falls just outside the transect zone.

In passing it may be noted that the sequence of westerly subtraction of eastern lowland taxa (Set 2) differs from the sequence given in Poynton 1990. In the latter paper, subtraction was traced across the continent in a due westerly direction, and took into account distribution on the southeastern lowlands of Zimbabwe.

In Table 2, the listing sequence of species in Set 1 follows the taxonomic order in earlier parts of this study. In the other sets, species are listed in a sequence from lesser to greater presumed range.

Except by collecting more records, it is not possible to test the assumptions implicit here that ranges grouped in Set 2 will not be shown to extend much further west, and that ranges grouped in Set 3 will not be shown to extend much further east. The degree of confidence that may be held regarding these assumptions can nevertheless be assessed to some extent, by evaluating the completeness of collecting data which is summarised in Table 3.

The lack of any records in a quarter-degree interval within the presumed range (shown as o in Table 2) could be a reflection either of a low intensity of collecting in the particular interval, or of low chances of collecting the particular species, as in the case of fossorial and rarely-emerging species. The intensity or success of collecting in each quarter-degree interval may be expressed as the percentage of positive species records in the interval, calculated by dividing the sum of + records by the sum of + and o entries in the interval. These percentages are shown in Table 3. It may be seen that only one quarter-degree interval (32° c) shows a value of 100 %, namely the interval in which Mutare and Inyanga are located. The

TABLE 3

Intensity (or success) of collecting in quarter-degree intervals from Chinhoyi to Beira.

30°				31°				32°				33°				34°			
a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
61	43	34	89	89	32	62	52	69	30	100	79	75	38	38	81	85	57	74	82
Chinhoyi				Harare		Marondera		Rusape		Mutare/Inyanga	Stapleford	Vila de Manica			Amatongas	Vila Machado		Dondo	Beira

data shown in Table 2 have to be evaluated bearing in mind this incompleteness of records.

The patterning of presumed range boundaries shown in Table 2 can be quantified by counting the number of such boundaries occurring in each quarter-degree interval within the transect zone. Given that there are 66 boundaries within the transect zone (including boundaries of disjunct populations), a uniform distribution of boundaries along the transect would give a score of a little over 3 (66/20) boundaries per interval, assuming uniform collecting intensity along the length of the transect. A tabulation of the number of boundaries occurring in each quarter-degree interval (Table 4) shows unevenness of occurrence, with very slight change in taxon composition on the interior plateau, but marked change on the mountainous edge to the plateau. Since this plateau edge includes the best collected interval of the transect, the intensity of collecting may be thought to have a bearing on the number of boundaries recorded in the sector; but a calculation of rank correlation between collecting intensity and number of recorded boundaries shows no significant overall relationship (r' = 0,46, n = 20).

If the taxon boundaries occurring in each quarter-degree interval (Table 4) are grouped according to the sets shown in Table 2, a pattern emerges which is shown in Table 5. The relatively large numbers of boundaries in intervals 32° c and d and

TABLE 4

Number of species boundaries occurring in each quarter-degree interval.

30°				31°				32°				33°				34°			
a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
2				1		1		3	3	11	12	7	2	1	5	9	3	4	2

TABLE 5

Number of species boundaries grouped according to sets in Table 2.

	30°				31°				32°				33°				34°			
Set	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
2									2		4	2	1	1	1	3	3	1	3	2
3	2				1		1		1		2	4	4	1		2	4	2	1	
4										3	5	6	2				2			

31° a indicate a very dynamic zoogeographical situation, with subtraction taking place both eastwards and westwards. Subtraction in both directions is also indicated on the Mozambique Plain (intervals 33° d and 34° a). The eastern lowlands set (Set 2) undergoes fairly steady subtraction across Mozambique and the eastern Zimbabwean highlands, with a major drop on encountering the interior plateau (32° c). The set soon peters out on the plateau. The plateau set (Set 3) appears to undergo heaviest subtraction where the eastern plateau slopes commence (32° d and 33° a). The result is a substantial overlap of Sets 2 and 3 in the eastern Zimbabwean highlands (32° c, d, 33° a). The interior plateau set peters out as the coastal lowland is traversed. The set of localised ranges (Set 4) is clustered in the eastern highlands, with an outlier in the Gorongoza Mountain (34° a). The occupation of the eastern highland zone by all four sets gives it the highest taxon diversity in the transect, as indicated in Table 6.

The effect of these subtractions on faunal composition may be gauged by estimating similarities between various intervals of the transect. Most convenient for this purpose is a similarity index variously attributed to Dice or to Sorenson (2 × no. taxa common to both areas/sum of totals of taxa in both areas), expressed as a percentage. Table 7 shows the results of some comparisons. A substantial turnover of taxa is indicated in Mozambique, which is consistent with the data in Tables 4 and 5, where more boundaries are shown to occur between Beira and Mutare than between Mutare and Chinhoyi.

It may be concluded that, despite the complexity of environmental and biological factors, the overall picture indicated in the Beira–Chinhoyi transect is fairly straightforward. The broad picture gained from the agglomerative classification of ranges in this study is corroborated by the transect, namely that distribution patterns in southeastern Africa resolve into units, a major feature of which is an overlapping of subtraction margins of lowland-centred and plateau-centred units, with a smaller unit located in the zone of overlap. Assignment of taxa to the various units differs slightly in the classification and the transect, which is an outcome of differing geographical limits. These differences do not however fully support Hengeveld's (1990: 48) assertion that 'classifications of the same general

TABLE 6

Taxon diversity (number of taxa in each quarter-degree interval), based on the 'presumed ranges' of the taxa (see text).

30°				31°				32°				33°				34°			
a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
36	35	35	35	35	34	34	33	35	37	43	42	36	32	32	36	40	37	38	39

TABLE 7

Percentage similarities (Dice-Sorenson) between transect intervals, based on 'presumed ranges'.

Transect intervals	% similarity
Chinhoyi (30° a) : Beira (34° d)	43
Chinhoyi : Mutare-Inyanga (32° c)	81
Mutare-Inyanga : Beira	54

area, but with dissimilar limits, will not be comparable'. If the statement were wholly true, then testing and corroboration of classifications would not be possible. Hengeveld (1990) himself discussed the use of transects as a means of testing classifications, and the present study shows their usefulness to be considerable, even when resorting to the rather coarse partitioning of a quarter-degree grid.

Environmental background

In the Introduction, it was suggested that beyond the task of identifying any discrete clusterings of species ranges was the objective of investigating the causal network behind the perceived pattern of distribution. In practice, an investigation of this kind tends to reduce itself to attempts to find correlations between distribution patterns of the group being studied and the distribution patterns of other organisms and of various climatic or other physical variables. Bearing in mind that correlation relates only to the degree of association between variables, and not necessarily to any causal relationships, a search for correlations need not necessarily be productive, particularly if no hypotheses regarding specific causal mechanisms are presented for testing. Writers on amphibian distribution, for example, generally recognise at least one group of 'forest species', but the association with forest may prove to be incidental (Poynton 1964*a* 1989). Species adapted primarily to living in fast-flowing streams may normally occur in forest, which tends to develop in association with such streams; but the species may be found at high altitudes where forest is replaced by grassland. Other species, such as those which lay eggs in seepage patches, may take advantage of the protection provided by tree cover against heat and desiccation; but their occurrence in grass-covered highlands again shows that they are not wholly reliant on tree cover. Yet other species lay eggs in humus or in shaded soft soil, which is a characteristic substrate of forests; but where forest has been cleared, such species can continue to breed if there is scrub or dense grass cover. It therefore seems to be of secondary importance whether or not the mesic conditions required by such species necessarily include the development of forest. For this reason, it seems, the finding of Happold & Happold (1989: 363) regarding Malaŵian small mammals, that 'forest species can survive in grasslands, but grassland species cannot survive in forest', broadly holds true also for amphibians.

Strictly speaking, a 'forest species' would be one whose life is specifically tied to the presence of a closed canopy of trees, in the sense that this community is the sole provider of a particular type of food, shelter, breeding site or other essential resource. While there are indications that the relatively mesic conditions provided by forest may allow some species to extend their ranges locally into hot lowland areas, as apparently in the case of *Arthroleptis xenodactyloides* discussed above (p. 227), it seems that *Stephopaedes anotis* may be the only species in the Zambesiaca area which is directly dependent on a forest resource, in that breeding takes place in treeholes sheltered by forest canopy. *Probreviceps rhodesianus* might be thought of as being dependent on tree cover, but the relatively primitive *Breviceps verrucosus* shows, in South Africa, an ability to breed in grassy areas cleared of forest (Poynton 1964*a*, Poynton & Pritchard 1976). The ecology of *P. rhodesianus* needs to be better known before the possibility of similar adaptability can be ruled out. *Arthroleptis francei* and *A. xenodactyloides* are normally found associated with forest, but individuals have been collected in dense grassland; it is not known whether *A. reichei* is more closely tied to a forest environment in some way. Among the 'treefrogs', only *Leptopelis flavomaculatus* has so far been found to have a tight association with the presence of trees or shrubs; yet breeding success in open situations need not be wholly discounted, bearing in mind the ability of the similar *L. natalensis* to breed in such situations in South Africa (Poynton 1964*a*).

This wide ecological tolerance, so typical of amphibian species, raises doubt about the fruitfulness of comparing species distributions with the detailed chorological analysis presented in Flora Zambesiaca (Wild and Barborosa 1967), even if the amphibian ranges were themselves known with exactness. The Flora Zambesiaca vegetation map largely followed a physiognomic classification, but the vegetational physiognomy that most amphibian species appear to respond to seems broader even than the classification adopted by White (1983); and the response to vegetation can be variable, as in cases just considered where 'forest' species occur in the open in upland situations.

It may be asked whether amphibian distribution, taken by itself, can provide any pointers to environmental factors that have had an effect on shaping distribution patterns. The occurrence of disjunctions in ranges is one case where pattern may be expected to be revealing of process. Major disjunctions are evident in the ranges of the following species and subspecies: *Scolecomorphus kirkii* (MZ), *Xenopus l. laevis* (S), *Arthroleptis xenodactyloides* (MZ), *Rana j. johnstoni* (MZ)—*R. j. inyangae* (EZ), *Strongylopus grayii rhodesianus* (EZ), *Strongylopus f. fasciatus* (EZ)—*S. fasciatus fuelleborni* (MZ), *Hylarana darlingi* (NW), *Ptychadena porosissima* (NW), *Ptychadena uzungwensis* (NW), *Ptychadena guibei* (NW), *Ptychadena taenioscelis* (NW), *Nothophryne broadleyi* (MZ), *Leptopelis bocagii* (NW), *Hyperolius puncticulatus* (MZ), *Hyperolius spinigularis* (MZ), *Hyperolius benguellensis* (NW), *Hyperolius marmoratus broadleyi* (C), *Bufo kisoloensis* (MZ), *Bufo gariepensis inyangae* (EZ)—*B. g. gariepensis* (S. Africa), and *Stephopaedes anotis* (EZ). It seems significant that no 'East African lowland' (EA) species appear in this list. In the case of the 'southern' (S) *Xenopus l. laevis*, an isolated population occurs on Inhaca Island; *X. muelleri* currently occupies the adjacent Mozambique Plain. This pattern suggests a former continuous distribution of *X. l. laevis* over the area, which would have been made possible by a lowering of sea level and a northward expansion of the range resulting from cooler conditions, such as would have occurred during the last glacial period (Poynton 1964*a*). *X. l. laevis* also has disjunct populations on the upland Shire and Nyika areas of Malaŵi (Poynton & Broadley 1985*a*). These populations could be relicts of the same northward expansion of range from southern Africa during the last glacial period. If temperature is the primary factor involved here, then it should be expected that the present retraction of range in this southern subspecies would be matched by range expansion in tropical species and subspecies. This appears to be so, in that no East African lowland species show major disjunctions at the present time.

No species of *Xenopus* have been found on the Bazaruto Archipelago, recently studied by one of us (DGB). The amphibians found there belong to species common on the adjacent mainland: *Phrynomerus bifasciatus*, *Tomopterna krugerensis*, *Ptychadena mossambica*, *Phrynobatrachus mababiensis*, *Leptopelis mossambicus*, *Kassina senegalensis*, *Hyperolius tuberilinguis* and *Hyperolius marmoratus taeniatus*. No reason can be found for the absence of *Xenopus*, *Breviceps* and *Bufo* on the archipelago.

In the case of the remaining species listed above as showing disjunctions, conformities again exist between distribution patterns and zonal temperature, associated with altitudinal and latitudinal gradients. Widespread species such as *Xenopus laevis*, *Strongylopus fasciatus*, *S. grayii* and several in the Northwestern Group (NW) have ranges which include the coastal lowland of at least the southern half of Natal, but which start veering off the lowland in northern Natal and beyond, becoming more or less restricted to upland areas. Restricted distributions in Afromontane areas have tended to attract particular attention in the literature, much of which has recently been reviewed in studies by Prigogine (1987) on birds and Happold & Happold (1989) on small mammals. Accumulating evidence that glacial periods were arid in intertropical Africa has led to a reconsideration of which palaeoenvironments would allow former range continuity in species which currently have disjunct or restricted upland distributions, especially those associated with forest. Prigogine (1987) has put forward a 'working hypothesis' that range continuity in such species could have occurred during especially humid interglacials, while Happold & Happold (1989: 364) suggest that a forest-grassland mosaic has always been present, and that this mosaic 'has moved up and down the mountains in response to fluctuations in climate'. Exactly which climatic factors could be involved are not specified.

Species such as *Arthroleptis xenodactyloides* provide possible evidence, just discussed, of range expansion into hot lowlands under cover of trees, which could allow range continuity during especially humid interglacial periods, in conformity with Prigogine's working hypothesis. But by and large, amphibian distribution patterns do not appear to offer specific tests for the hypotheses either of Prigogine or of Happold & Happold. Disjunctions do nevertheless suggest that ranges have 'moved up and down' in relation to altitude and latitude, in response to climatic fluctuations. This prepares the ground for setting up dynamic models which relate cyclic changes in climate to changing biogeographical patterns, notably relict and radial patterns (Poynton 1986).

Precise identification of the factors in climatic fluctuations that may result in the movement of ranges 'up and down' in relation to altitude and latitude may, however, prove to be defeated by the sheer complexity of the situation. A perceived conformity between amphibian distribution and thermal patterns has led to a few attempts to identify causal relationships, by pointing out correlations between the two. It could be expected that virtually any measure of thermal patterning, whether of mean midwinter month temperatures (Poynton 1964*a*), number of tropical nights per year (Poynton 1969), or a formula for effective temperature (Stuckenberg 1969), will show some correlation with amphibian distribution; yet it is not certain how far precise correlations between climatic patterns and distribution may be expected even to exist. For example, a lag may be expected to occur between climatic change and any resulting change in species ranges. This lag would be complex, being governed largely by the environmental tracking rate of each species. In the case of Holocene warming, the likely effect would be a spread in the ranges of tropical species, which at any particular moment would have the appearance of a diffusion gradient, being strongly affected by the individual tracking rate of each species. The resulting gradient of declining species diversity need bear no detailed relationship with any particular environmental pattern.

In his recent study of vertebrate distribution over southern Africa, Crowe (1990) found in a regression analysis that a combination of mean annual rainfall and mean midwinter (July) temperature accounted for 79 % of the geographical variation in amphibian species richness over the subcontinent (rainfall 57 % positive relation; temperature 22 % positive relation). The inclusion of the arid west in Crowe's survey area results in an understandably high value for the rainfall relationship, which may not hold for the Zambesiaca area. The large size of the grid-quadrats used in Crowe's analysis limits its application to an area of the size covered in the present study, but our analysis does not confirm Fig. 3b in Crowe's study, which shows a 50 % drop in species richness at about 24° E compared with the eastern coastal lowlands. The region marked in Crowe's Fig. 3a as being the 'base of the arid corridor' is in fact a region reached by several 'East African lowland' species extending up the Zambezi Basin (Poynton 1964*a*). At 24° E around the latitude of Beira (20° S), the region has a count of 31 taxa, which is 79 % of the East African lowland cluster (EA) recognised in the present study. The percentage species/subspecies similarity between this region and the Beira area is 54 %. This is in fact greater than the similarity between Beira and Chinhoyi (43 %, Table 7), which is placed on the plateau between Beira and the interior Zambezi basin. Lower temperatures on the plateau correlate with this pattern, but until more is known of the biology of the species involved, nothing definite can be proposed.

CONCLUSION

So far, research has yielded little more than mere indications of how complex the relationship between environment and distribution must be, and how large are the gaps in our knowledge of palaeoenvironments and of relevant amphibian biology in all aspects from breeding behaviour through larval ecology to adult ecology (Poynton 1988). Pointers provided by distributions themselves are not always clear. Thus there is some evidence that range expansion of East African lowland species is still taking place at least in Zimbabwe (Poynton & Broadley 1978); yet the scattered or disjunct distributions of *Ptychadena guibei* and *P. taenioscelis*, on the other hand, can be seen to indicate retraction in the ranges of species formerly widespread in tropical areas. Available records for many *Ptychadena* species tend to be patchy, however, and it is not clear whether the present picture results from inadequate sampling of easily overlooked species, or from actual population fragmentation.

Such uncertainty is all part of 'the general incompleteness of our present knowledge' regarding amphibians in the area, which was noted in the Introduction to Part 1 of this series (Poynton & Broadley 1985*a*). In this concluding Part, the incompleteness of our knowledge regarding species ranges is especially evident; zoogeographical treatment can go little further without the acquisition of more locality records. These records may be obtained more easily by sampling tadpole rather than adult populations, and the recent guide by Lambiris (1989) provides a start in this direction. In addition to the need for more locality records, an adequate treatment of the zoogeography of the area requires better developed taxonomic and phylogenetic understanding, and also it requires sets of environmental (especially climatic) data of sufficient density to fill at least quarter-degree partitioning of wide regions. The success of the Amphibia Zambesiaca series will, we believe, prove to be largely measurable in terms of the stimulus and direction that it gives to further work on the amphibians and the environment of this part of Africa.

ACKNOWLEDGEMENTS

We are grateful to Dr B. R. Stuckenberg and Mr A. J. L. Lambiris for critical readings of drafts of this paper and for valuable discussion. The University of Natal has contributed to printing costs, and, with the Foundation for Research and Development, Pretoria, has contributed to other costs, notably travel. We are again indebted to Dr B. T. Clarke, of the British Museum (Natural History), for his ready assistance in many ways.

REFERENCES

Alexander, G. J. 1989. The use of a multivariate method of classification (two-way indicator species analysis) in biogeography. *Herp. Assoc. Afr.* **36**: 7–10.

Brown, J. H. 1988. Species diversity. *In*: Myers A. A. & Giller P. S. eds. *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. London: Chapman & Hall: 57–89.

Brundin, L. Z. 1981. Croizat's panbiogeography versus phylogenetic biogeography. *In*: Nelson G. & Rosen D. E. eds. *Vicariance biogeography: a critique*. New York: Columbia University Press: 94–138.

Channing, A. 1981. Southern origin of the African genus *Strongylopus* Tschudi, 1838 (Amphibia Ranidae). *Monitore zool. ital.* (N.S.) Suppl. **15** (15): 333–336.

——— 1989. New frog records from the Eastern Caprivi Strip, South West Africa/Namibia. *Madoqua* **16**: 1–4.

Croizat, L. 1968. Introduction raisonée à la biogéographie de l'Afrique. *Mems Soc. broteriana* **20**: 1–451.

Crowe, T. M. 1990. A quantitative analysis of patterns of distribution, species richness and endemism in southern African vertebrates. *In*: Peters G. & Hutterer R. eds. *Vertebrates in the tropics*. Bonn: Museum Alexander Koenig: 145–160.

Happold, D. C. D. & Happold, M. 1989. Biogeography of montane small mammals in Malaŵi, Central Africa. *J. Biogeogr.* **16**: 353–367.

Hengeveld, R. 1990. *Dynamic biogeography*. Cambridge: Cambridge University Press.

Humphries, C. J., Ladiges, P. Y., Roos, M. & Zandee, M. 1988. Cladistic biogeography. *In*: Myers A. A. & Giller P. S. eds. *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. London: Chapman & Hall: 371–404.

Jacobsen, N. G. H. 1990. *A herpetological survey of the Transvaal*. Unpublished Ph.D. thesis. Durban: University of Natal.

Lambiris, A. J. L. 1989. *The frogs of Zimbabwe*. Turin: Museu Regionale di Scienzi Naturali.

Loveridge, A. 1937. Scientific results of an expedition to rain forest regions in eastern Africa. IX. Zoogeography and itinerary. *Bull. Mus. comp. Zool.* **79**: 479–541.

McCoy, E. D., Bell S. S. & Walters, K. 1986. Identifying boundaries along environmental gradients. *Ecology* **67**: 749–759.

Myers, A. A. & Giller, P. S. 1988. Biogeographic patterns: Introduction. *In*: Myers A. A. & Giller P. S. eds. *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. London: Chapman & Hall: 15–21.

Owen, J. G. 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. *J. Biogeogr.* **16**: 141–150.

Parker, H. W. 1932. Two collections of reptiles and amphibians from British Somaliland. *Proc. zool. Soc. Lond.* **1932**: 335–367.

Perret, J. L. 1987. A propos de *Ptychadena schillukorum* (Werner, 1907) (Anura, Ranidae). *Bull. Soc. neuchât. Sci. nat.* **110**: 63–70.

Popper, K. 1972. *Conjectures and refutations.* (4th edn) London: Routledge & Kegan Paul.

Poynton, J. C. 1962. Zoogeography of eastern Africa: an outline based on anuran distribution. *Nature* **194**: 1217–1219.

——— 1964*a*. The Amphibia of southern Africa: a faunal study. *Ann. Natal Mus.* **17**: 1–334.

——— 1964*b*. Amphibia of the Nyasa-Luangwa region of Africa. *Senck. biol.* **45**: 193–225.

——— 1969. Optimum temperatures and amphibian distribution in south-east Africa. *Palaeoecol. Afr.* **4**: 161–162.

——— 1986. Historical biogeography: theme and South African variations. *Palaeoecol. Afr.* **17**: 139–153.

——— 1988. Amphibian distribution: facts in search of Quaternary theory. *Palaeoecol. Afr.* **19**: 327–333.

——— 1989. Biogeography of forest Amphibia. *In*: Geldenhuys C. J. ed. *Biogeography of the mixed evergreen forests of southern Africa*. Occasional Report No 45. Pretoria: CSIR.

——— 1990. Composition and subtraction patterns of the East African lowland amphibian fauna. *In*: Peters G. & Hutterer R. eds. *Vertebrates in the tropics*. Bonn: Museum Alexander Koenig: 285–296.

——— in press. Amphibians of southeastern Tanzania, with special reference to *Stephopaedes* and *Mertensophryne* (Bufonidae). *Bull. Mus. comp. Zool.*

Poynton, J. C. & Broadley, D. G. 1978. The herpetofauna. *In*: Werger M. J. A. ed. *Biogeography and ecology of southern Africa*, vol 2. The Hague: Junk: 927–948.

——— 1985*a*. Amphibia Zambesiaca 1. Scolecomorphidae, Pipidae, Microhylidae, Hemisidae, Arthroleptidae. *Ann. Natal Mus.* **26**: 503–553.

——— 1985*b*. Amphibia Zambesiaca 2. Ranidae. *Ann. Natal Mus.* **27**: 115–181.

——— 1987. Amphibia Zambesiaca 3. Rhacophoridae and Hyperoliidae. *Ann. Natal Mus.* **28**: 161–299.

——— 1988. Amphibia Zambesiaca 4. Bufonidae. *Ann. Natal Mus.* **29**: 447–486.

Poynton, J. C. & Pritchard, S. 1976. Notes on the biology of *Breviceps* (Anura: Microhylidae). *Zool. Afr.* **11**: 313–318.

Prigogine, A. 1987. Disjunctions of montane forest birds in the Afrotropical Region. *Bonn. zool. Beitr.* **38**: 195–207.

Sattler, R. 1986. *Biophilosophy: analytic and holistic perspectives*. Berlin: Springer-Verlag.

Schiøtz, A. 1975. *The treefrogs of eastern Africa*. Copenhagen: Steenstrupia.

——— 1976. Zoogeographical patterns in the distribution of East African treefrogs (Anura: Ranidae). *Zool. Afr.* **11**: 335–338.

——— 1981. The Amphibia in the forested basement hills of Tanzania: a biogeographical indicator group. *Afr. J. Ecol.* **19**: 205–207.

Stuckenberg, B. R. 1969. Effective temperature as an ecological factor in southern Africa. *Zool. Afr.* **4**: 145–197.

Van den Elzen, P. & Kreulen, D. A. 1979. Note on the vocalisations of some amphibians from the Serengeti National Park, Tanzania. *Bonn. zool. Beitr.* **30**: 385–403.

White, F. 1978. The Afromontane Region. *In*: Werger M. J. A. ed. *Biogeography and ecology of southern Africa*, vol.1. The Hague: Junk: 463–513.

——— 1983. *UNESCO/AETFAT/UNSO vegetation map of Africa.* Oxford: Aetfat Vegetation Map Committee.

Wild, H. & Barborosa, L. A. G. 1967. *Vegetation map of the Flora Zambesiaca area.* Harare: M. O. Collins.

Date received: 4 February, 1990.

APPENDIX

Locality records not included in Parts 1 to 4

Material in the Natural History Museum of Zimbabwe, Bulawayo.

Xenopus laevis laevis Mvuradona Farm
Xenopus laevis petersii Hillwood Farm N; Nxaraga
Xenopus muelleri Chirundu; Majoda

Phrynomerus bifasciatus bifasciatus Benguera Island; 5 km S Chirundu; Kazuma Depression

Breviceps ? mossambicus Hillwood Farm S

Hemisus marmoratus marmoratus Chisuma River; Doddieburn Ranch; Hillwood Farm N; Mvuradona Farm

Arthroleptis stenodactylus Mavuradonna W.A.

Arthroleptis xenochirus Zambezi Rapids

Tomopterna cryptotis Seronga

Tomopterna marmorata Chisuma River

Rana angolensis Hillwood Farm S; Mavuradonna W.A.

Hylarana darlingi Hillwood Farm N; Isombo Stream; Mvuradona Farm; Mandala Dam; Zambezi Rapids

Hylarana lemairei Zambezi Source

Ptychadena oxyrhynchus Gutu Mission; Hillwood Farm S; Mvuradona Farm

Ptychadena anchietae Humani Ranch; Mavuradonna W.A.; Tuli

Ptychadena uzungwensis Hillwood Farm S

Ptychadena bunoderma Zambezi Rapids

Ptychadena taenioscelis Sakeji School; Zambezi Rapids

Ptychadena guibei Hillwood Farm N; Mushishima Farm

Ptychadena keilingi Hillwood Farm N

Phrynobatrachus natalensis Boatle Dam; Bumboosie River; Dwala Ranch; Hillwood Farm N; Kalomo; Magobane Dam; Mavuradonna W.A.; Pandametenga; Vale Farm

Phrynobatrachus mababiensis Banguerua Island; Bazaruto Island; Doddieburn Ranch; Hillwood Farm N; Mavuradonna W.A.; Mvuradona Farm

Phrynobatrachus parvulus Chirinda Forest; Zambezi Rapids

Cacosternum boettgeri Esigodini

Chiromantis xerampelina 5 km S Chirundu; Mavuradonna W.A.

Leptopelis mossambicus Bazaruto Island

Leptopelis bocagii Hillwood Farm S

Leptopelis cynnamomeus Isombo Stream

Kassina kuvangensis Hillwood Farm N

Kassina senegalensis Bazaruto Island; Sakeji School

Hyperolius tuberilinguis Bazaruto Island

Hyperolius quinquevittatus quinquevittatus Hillwood Farm S; Zambezi Rapids

Hyperolius marmoratus taeniatus Benguera Island

Hyperolius marmoratus broadleyi St Michaels School, Mutasa C.L.

Hyperolius marmoratus rhodesianus Kasetsheti River; Pandamatenga

Hyperolius marmoratus alborufus Hillwood Farm N & S; Zambezi Rapids

Hyperolius marmoratus angolensis Seronga

Bufo gutturalis Hillwood Farm S; Mavuradonna W.A.

Bufo garmani Bobonong; 5 km S Chirundu; Chisuma

Bufo maculatus 5 km S Chirundu; Chisuma River; Mushishima Farm

Bufo fuliginatus Zambezi Rapids

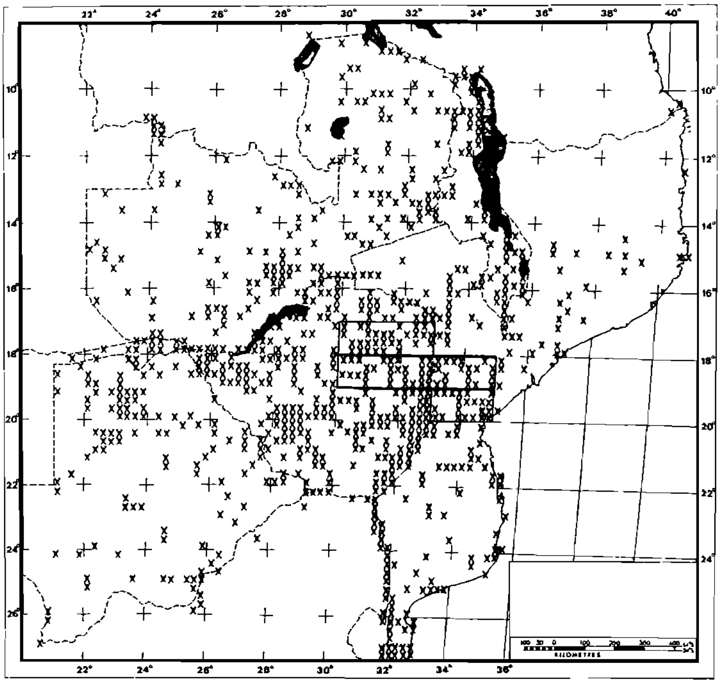
Bufo lemairii Nxaraga Lediba

Bufo fenoulheti fenoulheti Tuli

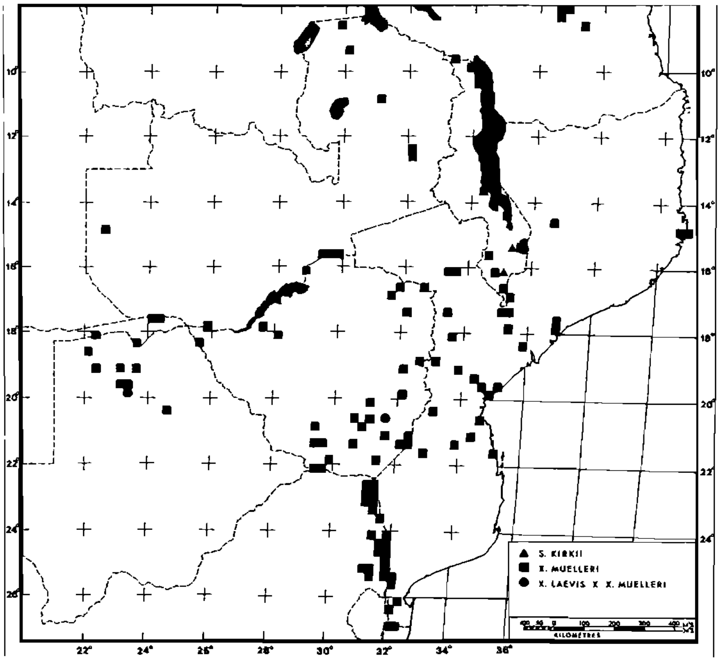
Schismaderma carens Mavuradonna W.A.

Gazetteer

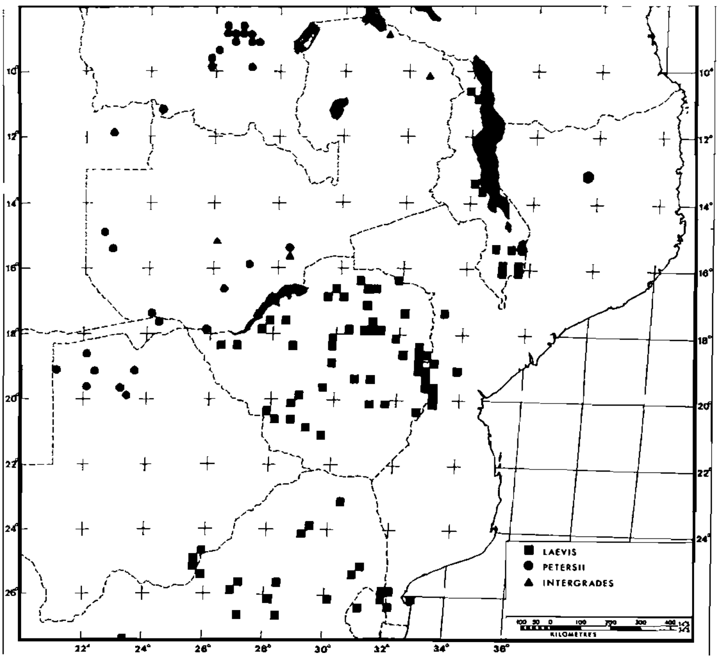
Locality	Country	Quarter-degree Grid Reference
Bazaruto Island	MO	2135 C2
Benguerua Island	MO	2135 C4
Boatle Dam	BO	2425 D4
Bobonong	BO	2128 C4
Bumboosie River	ZW	1826 C1
Chirinda Forest	ZW	2032 B3
Chirundu	ZW	1628 B2
Chirundu, 5 km S of	ZW	1628 B2
Chisuma	ZW	1825 B2
Chisuma River	ZW	1825 B2
Doddieburn Ranch	ZW	2129 A4
Dwala Ranch	ZW	2129 B1
Esigodini	ZW	2028 B4
Gutu Mission	ZW	1931 C1
Hillwood Farm N	ZA	1124 A2
Hillwood Farm S	ZA	1124 A4
Humani Ranch	ZW	2032 C2
Isombo Stream	ZA	1124 A3
Kalomo	ZA	1726 A2
Kasetsheti River	ZW	1825 B3
Kazuma Depression	BO	1825 B3
Kemavanga Stream	ZW	1631 A3
Magobane Dam	BO	2425 D3
Majoda	ZW	2029 C4
Mandala Dam	ZA	1627 C1
Mavuradonna W.A.	ZW	1631 A3
Mushishima Farm	ZA	1227 D2
Mvuradona Farm	ZW	1631 C1
Nxaraga Lediba	BO	1923 C1
Pandamatenga	ZW	1825 D1
St Michaels School	ZW	1832 D1
Sakeji School	ZA	1124 A2
Seronga	BO	1822 C4
Tuli	ZW	2129 C3
Vale Farm	ZW	1731 B3
Zambezi Rapids	ZA	1124 A1
Zambezi Source	ZA	1124 A4



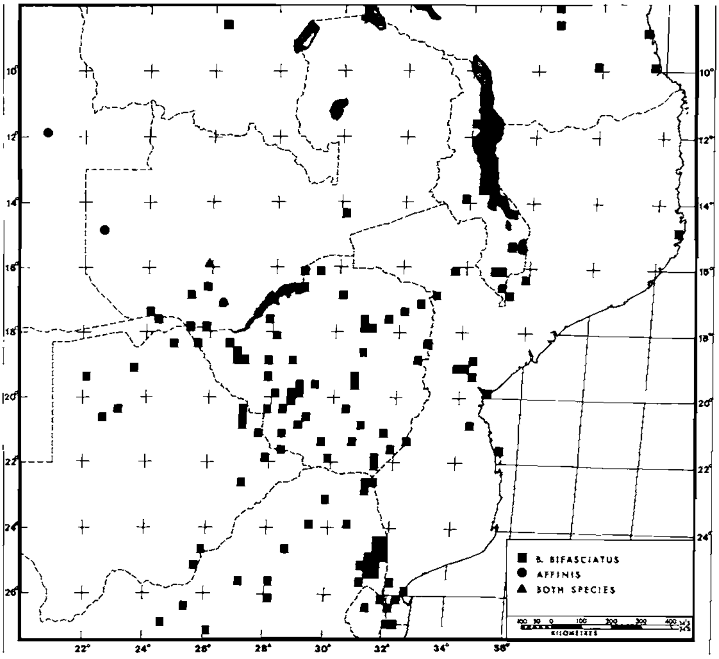
Map 1. Distribution of collecting in the Zambesiaca area and its fringes. Every quarter-degree square from which one or more specimens have been collected has been filled in.



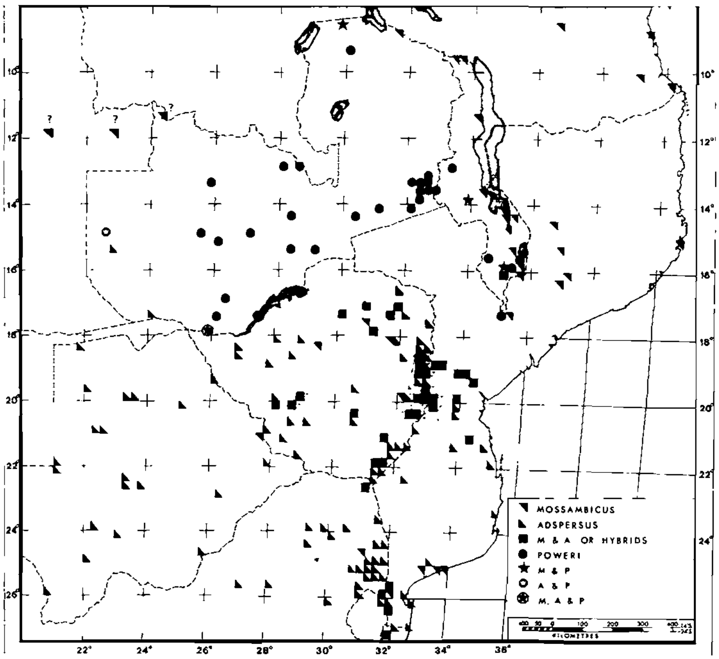
Map 2. *Scolecomorphus kirkii*, *Xenopus muelleri*, *X. laevis* × *X. muelleri*.



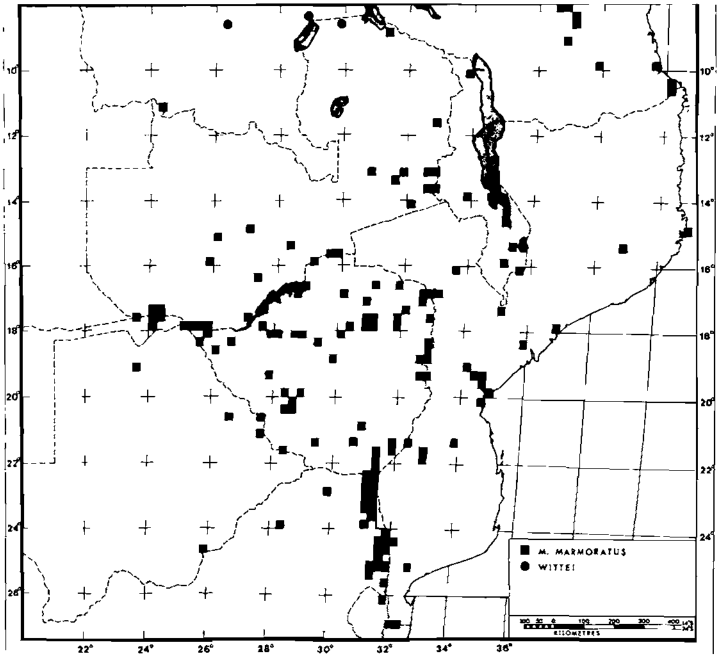
Map 3. *Xenopus l. laevis*, *Xenopus l. petersii*, *X. l. laevis—l. petersii* intergrades.



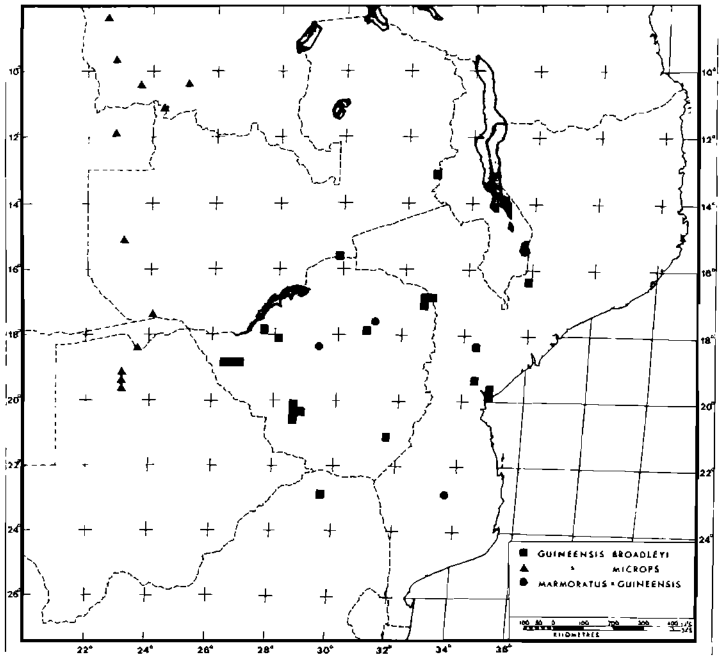
Map 4. *Phrynomerus b. bifasciatus*, *P. affinis*.



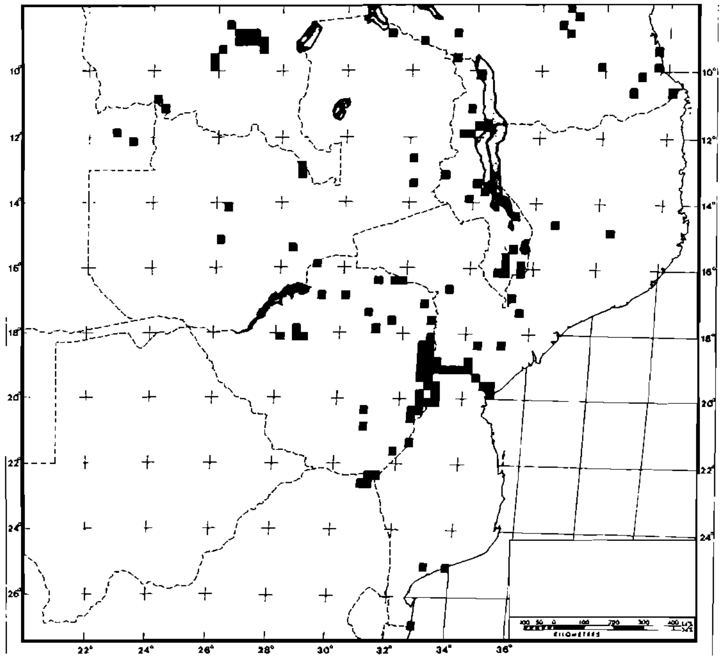
Map 5. *Breviceps mossambicus*, *B. adspersus*, *B. mossambicus* × *B. adspersus*, *B. poweri*.



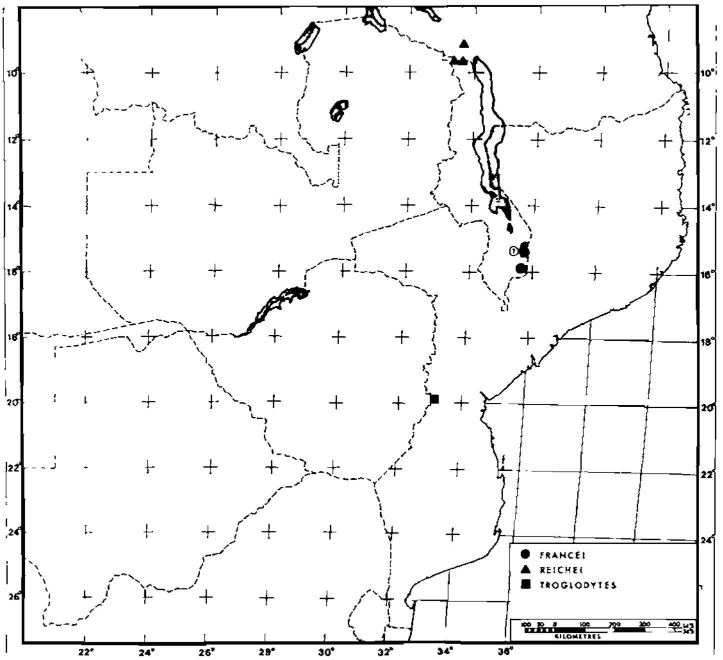
Map 6. *Hemisus m. marmoratus*, *H. wittei*.



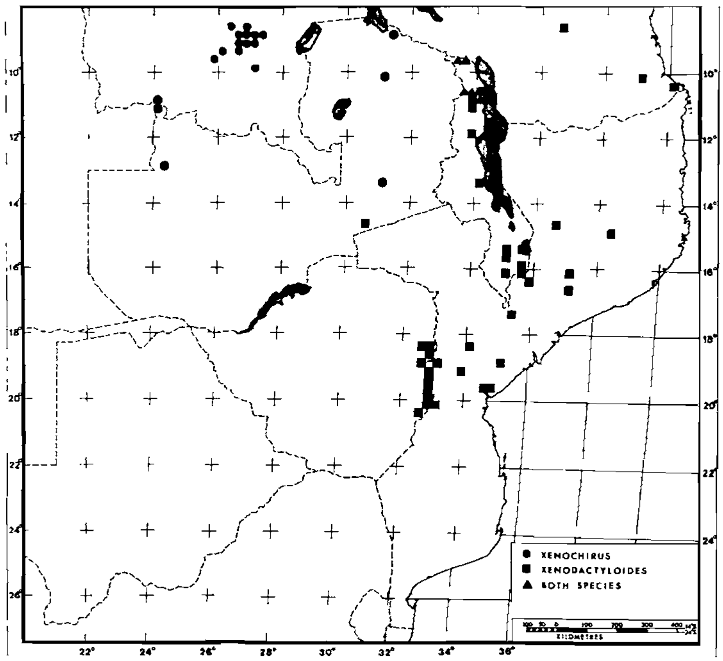
Map 7. *Hemisus guineensis broadleyi*, *H. g. microps*, *H. marmoratus* × *H. guineensis*.



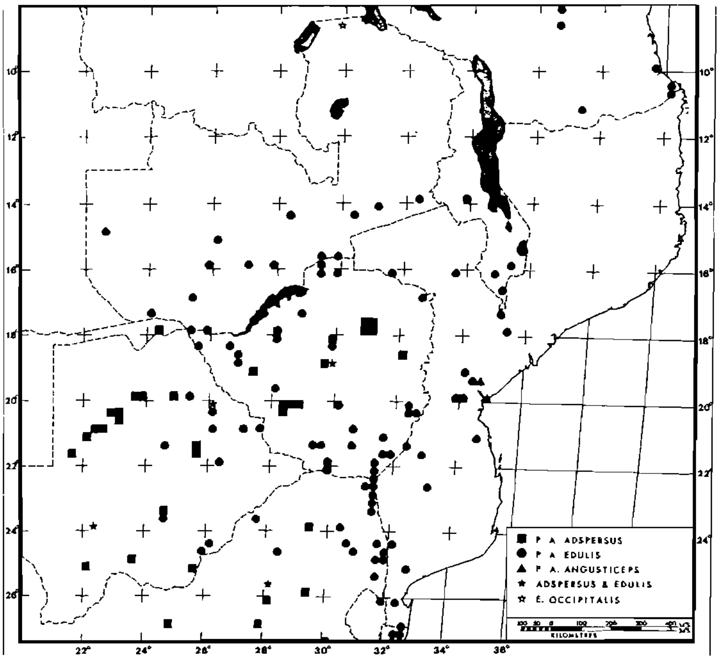
Map 8. *Arthroleptis stenodactylus*.



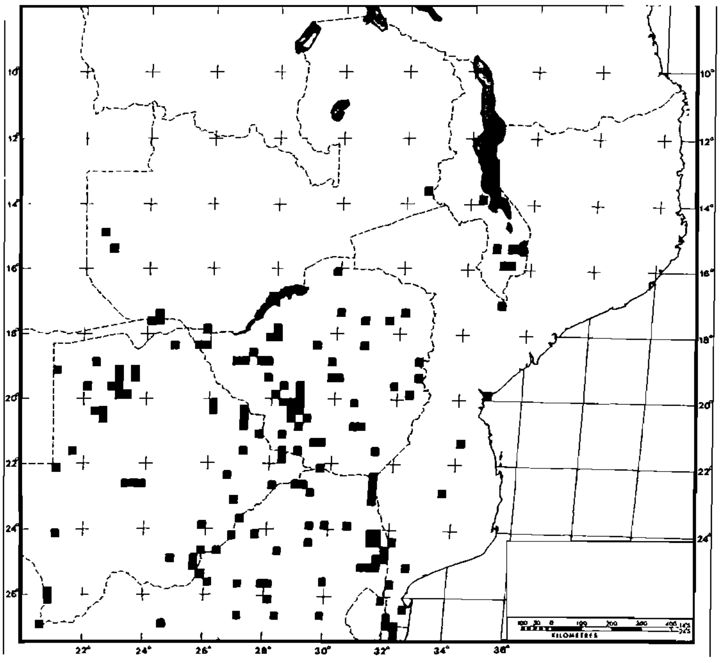
Map 9. *Arthroleptis francei*, *A. reichei*, *A. troglodytes*.



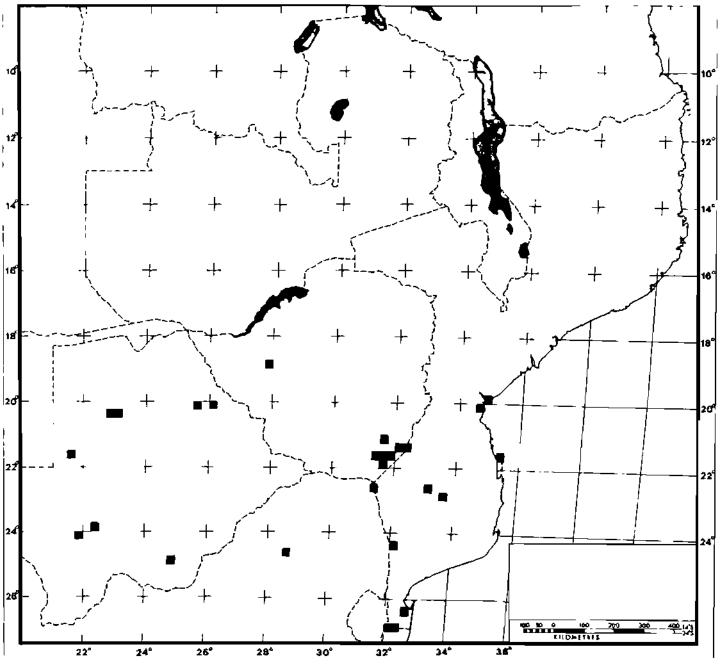
Map 10. *Arthroleptis xenochirus*, *A. xenodactyloides*.



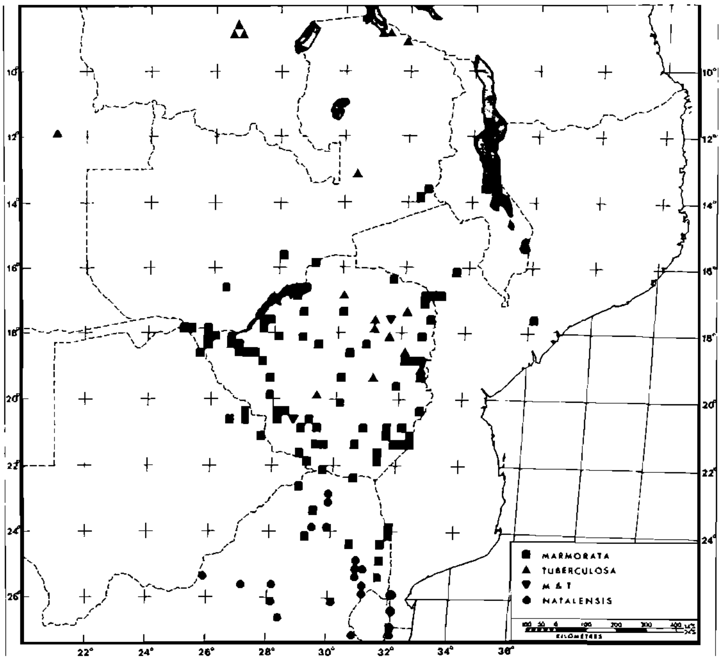
Map 11. *Pyxicephalus adspersus adspersus*, *P. a. edulis*, *P. a. angusticeps*, *Euphylctis occipitalis*.



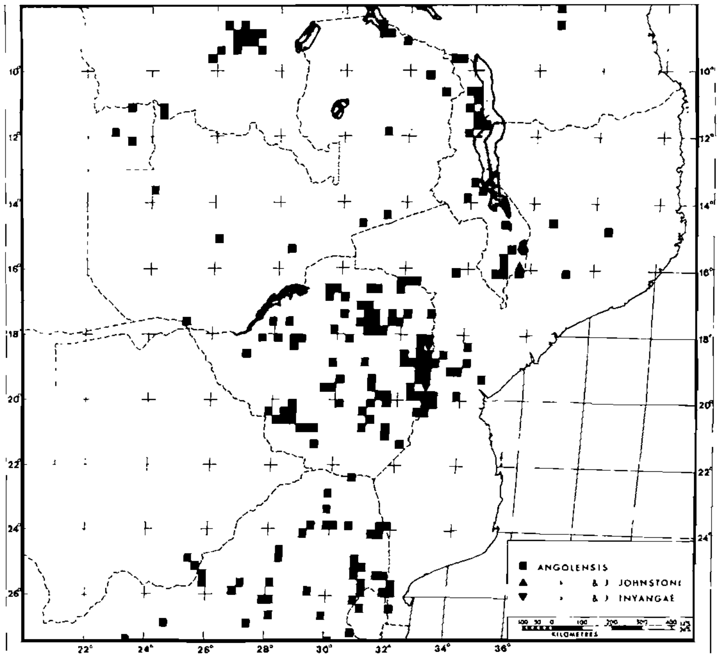
Map 12. *Tomopterna cryptotis*.



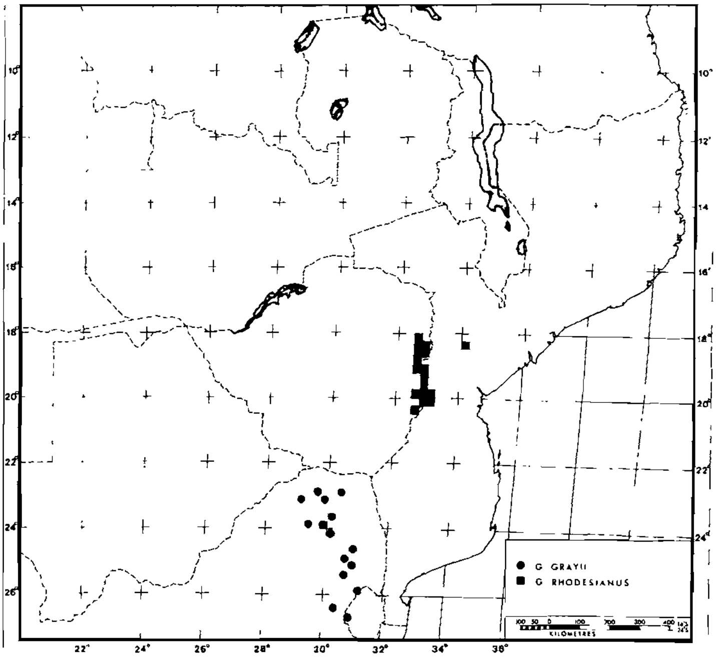
Map 13. *Tomopterna krugerensis.*



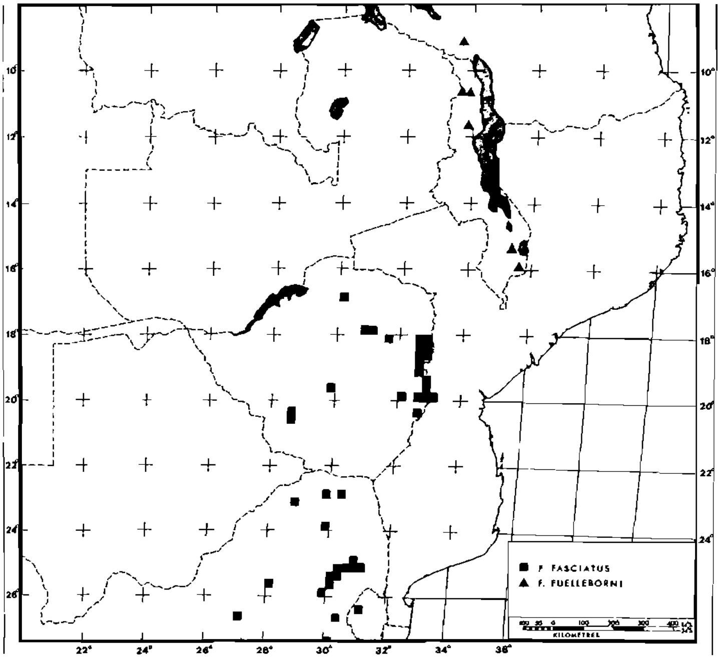
Map 14. *Tomopterna marmorata, T. tuberculosa, T. natalensis.*



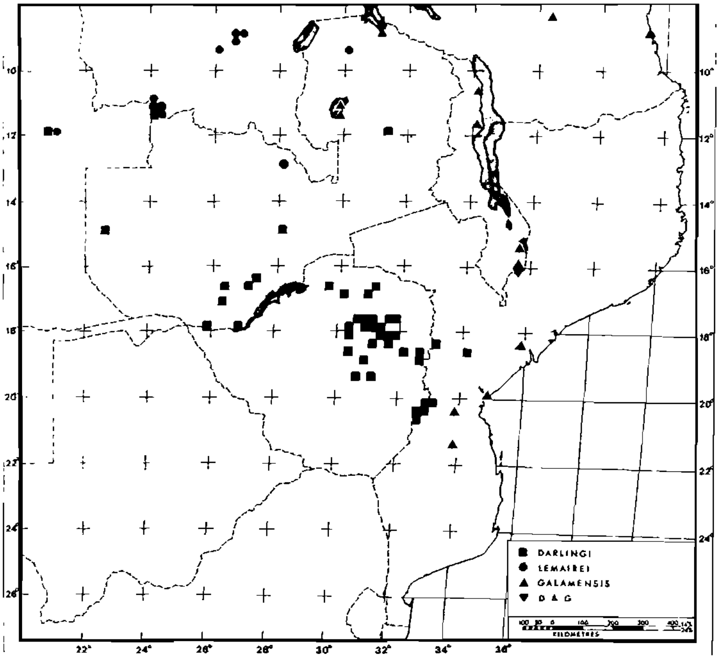
Map 15. *Rana angolensis*, *R. j. johnstoni*, *R. j. inyangae*.



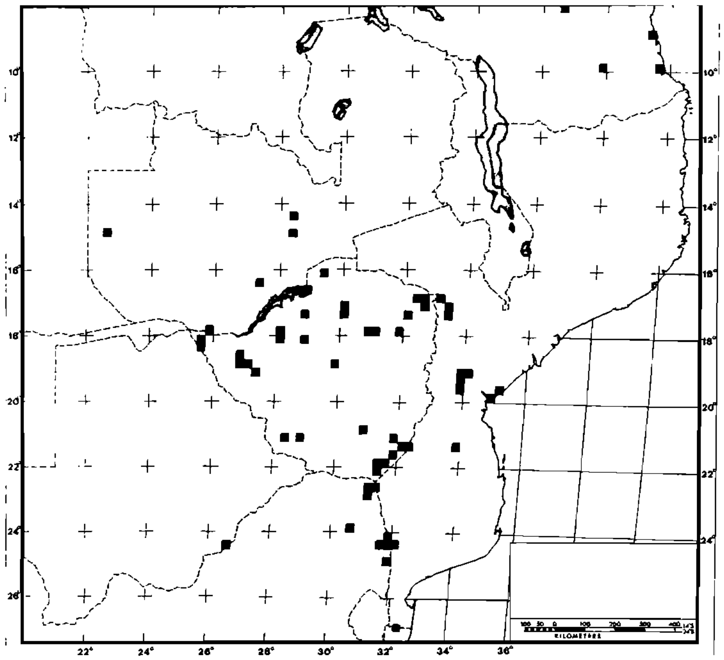
Map 16. *Strongylopus g. grayii*, *S. g. rhodesianus*.



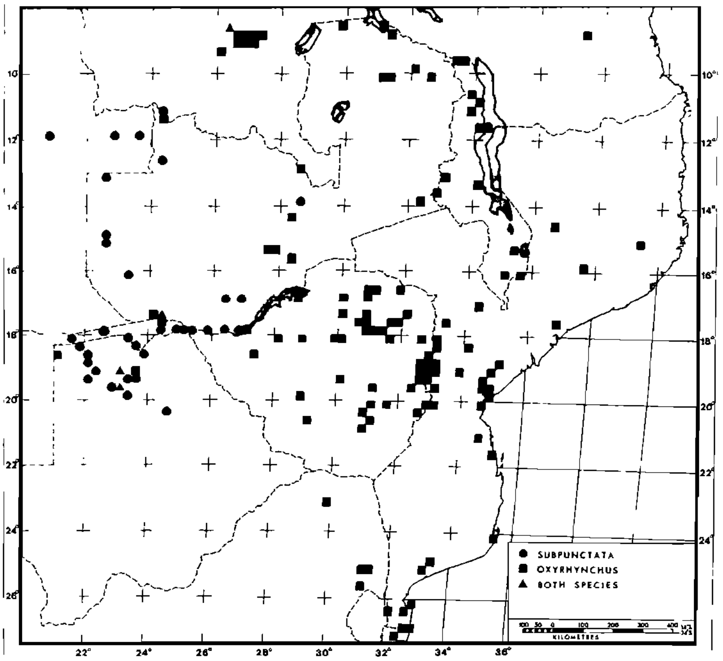
Map 17. *Strongylopus f. fasciatus*, *S. f. fuelleborni*.



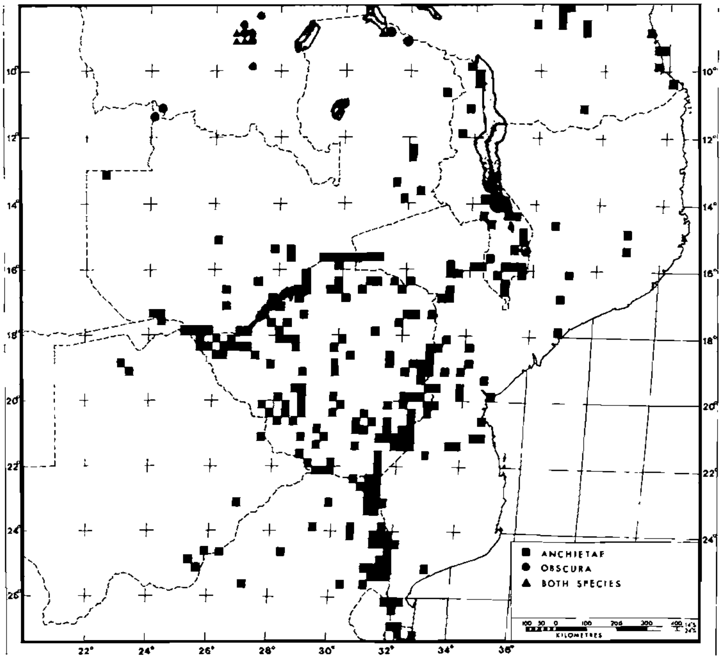
Map 18. *Hylarana darlingi*, *H. lemairei*, *H. galamensis*.



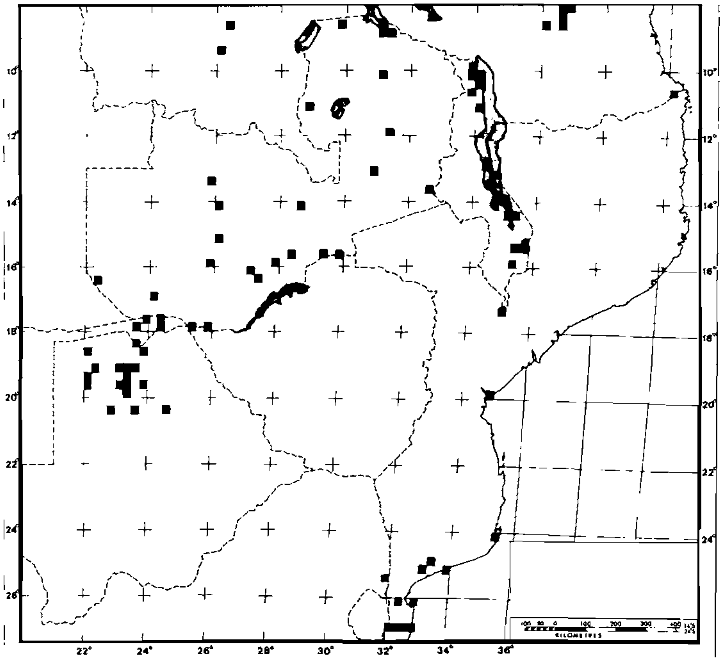
Map 19. *Hildebrandtia o. ornata*.



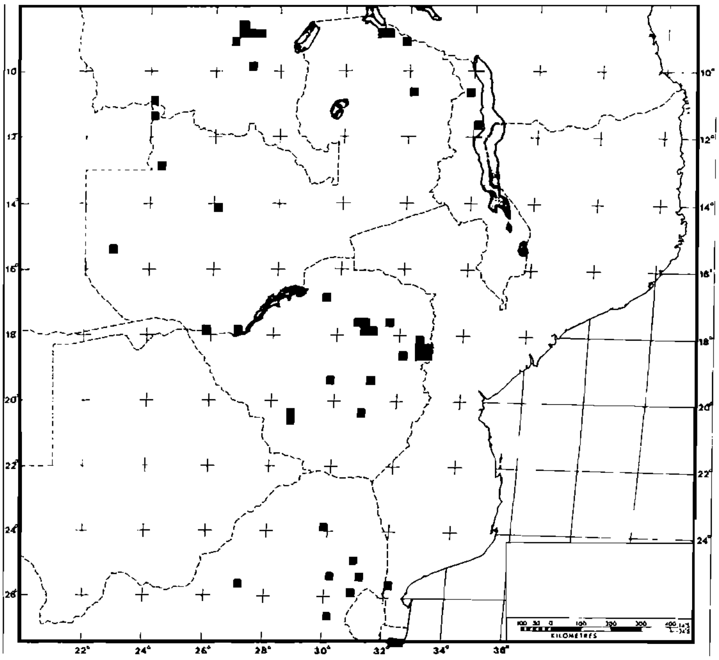
Map 20. *Ptychadena subpunctata*, *P. oxyrhynchus*.



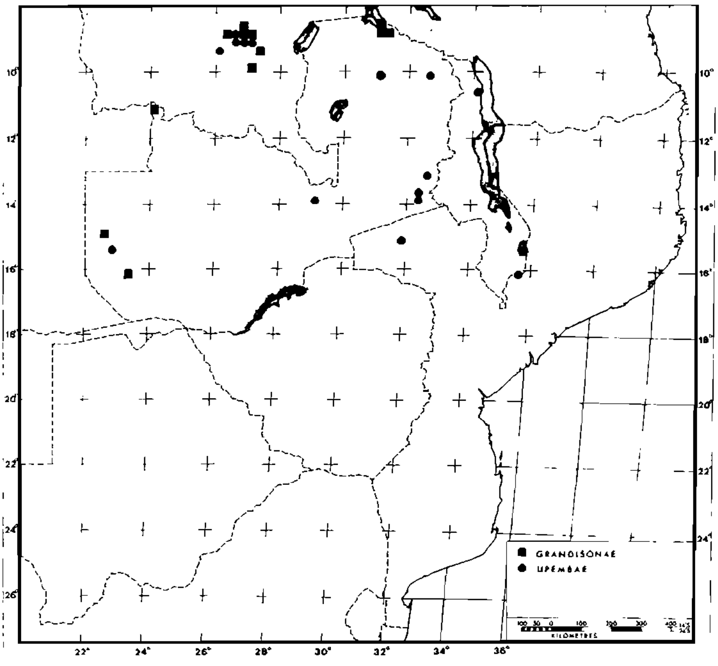
Map 21. *Ptychadena anchietae*, *P. obscura*.



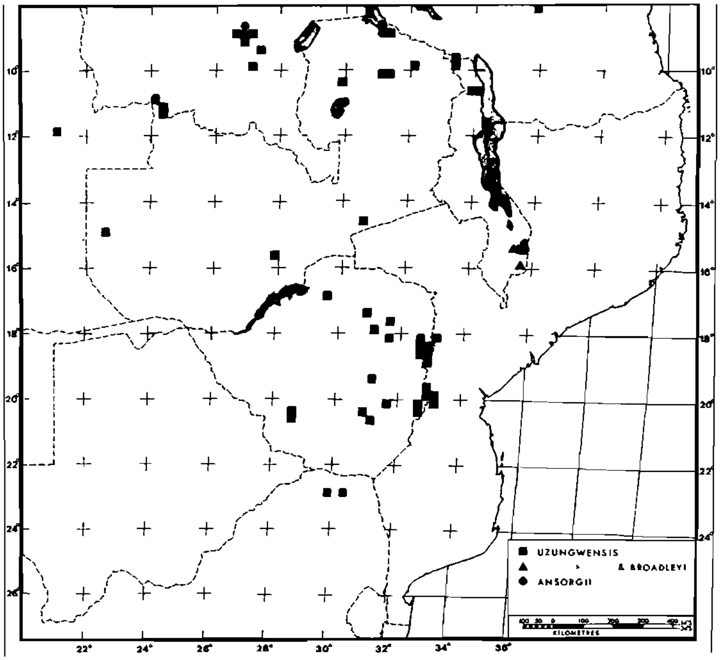
Map 22. *Ptychadena m. mascareniensis*.



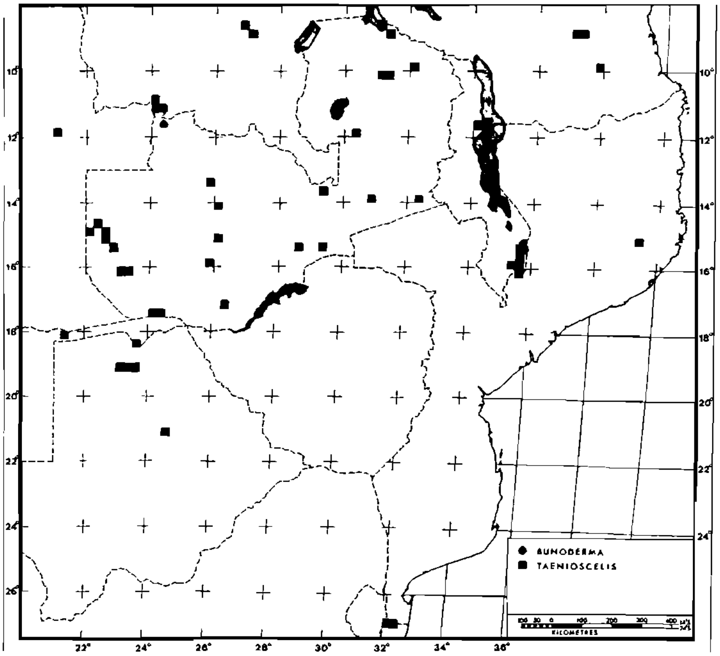
Map 23. *Ptychadena porosissima*.



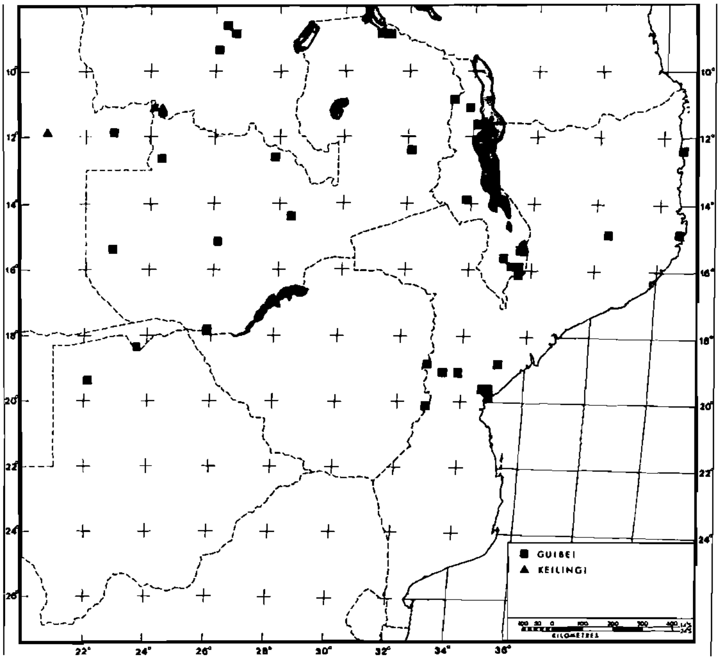
Map 24. *Ptychadena grandisonae*, *P. upembae*.



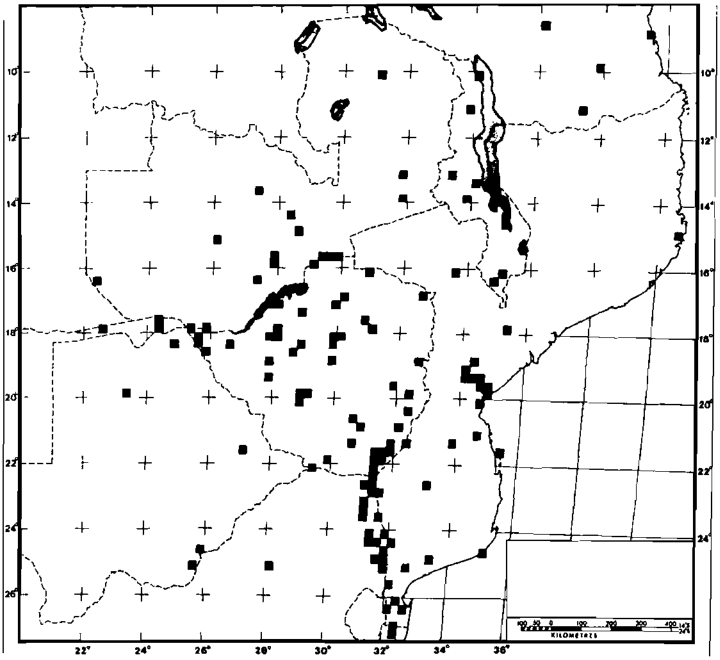
Map 25. *Ptychadena uzungwensis*, *P. broadleyi*, *P. ansorgii*



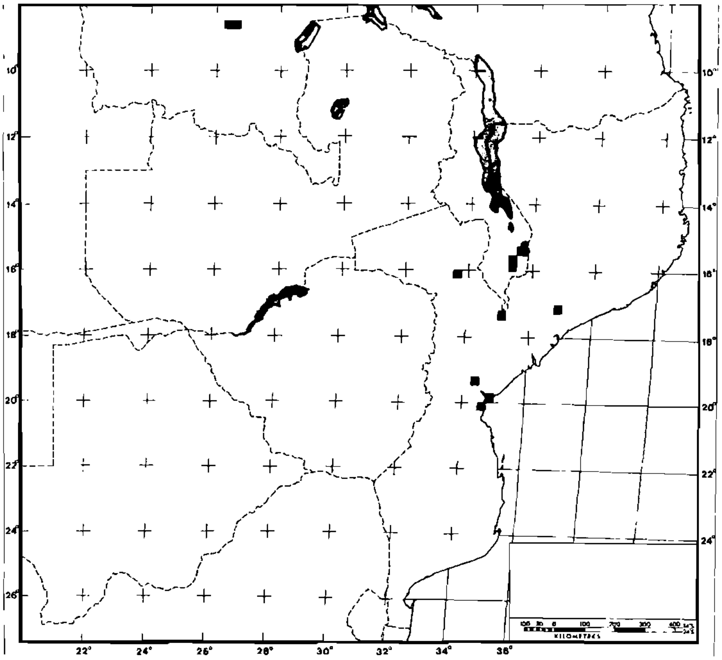
Map 26. *Ptychadena bunoderma*, *P. taenioscelis*.



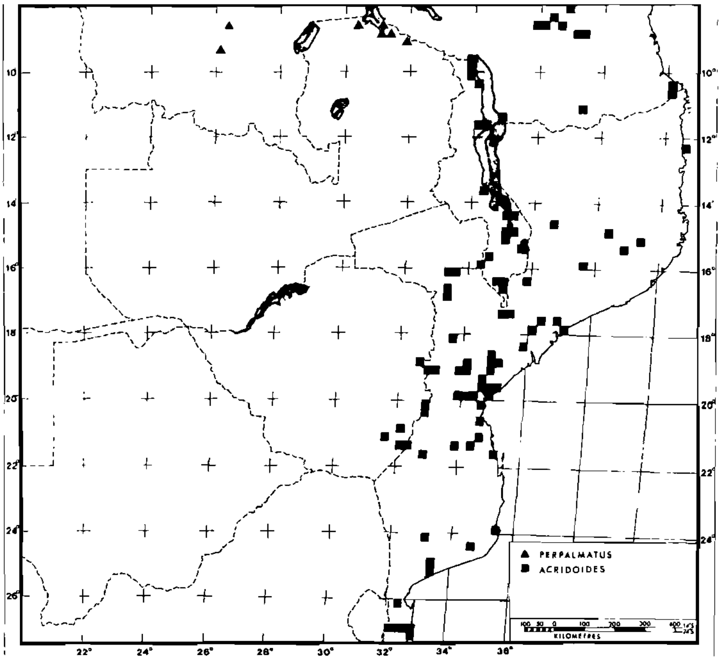
Map 27. *Ptychadena guibei*, *P. keilingi*.



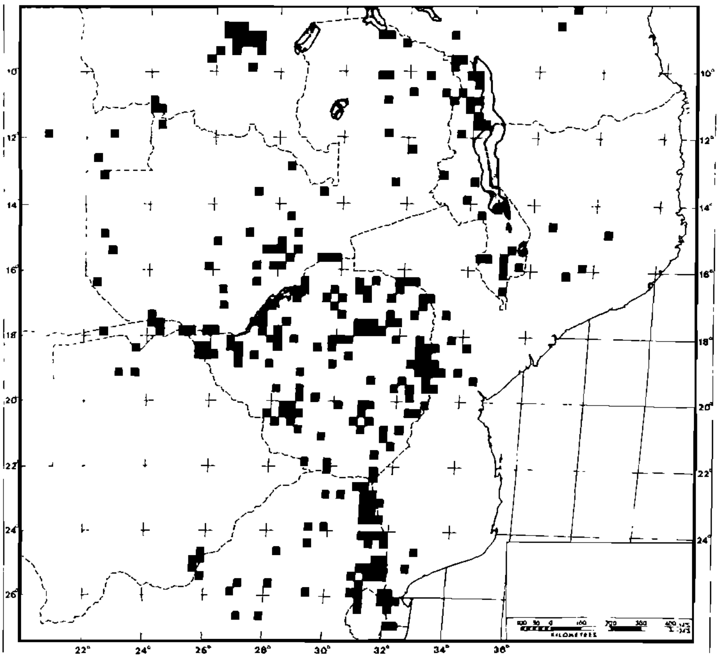
Map 28. *Ptychadena mossambica*.



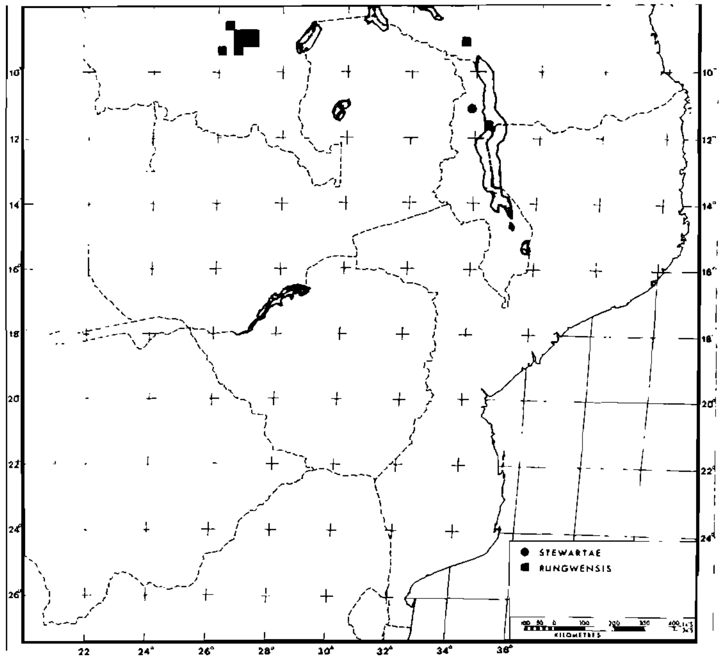
Map 29. *Ptychadena schillukorum.*



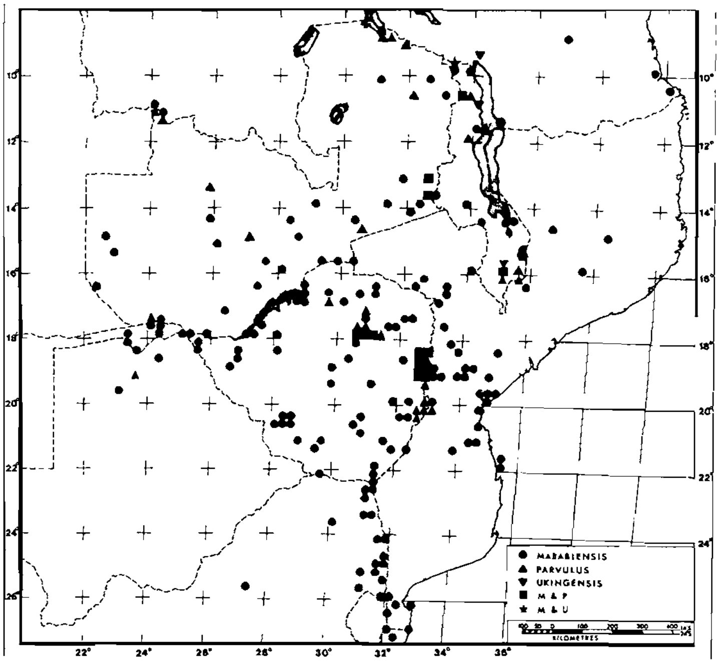
Map 30. *Phrynobatrachus perpalmatus*, *P. acridoides.*



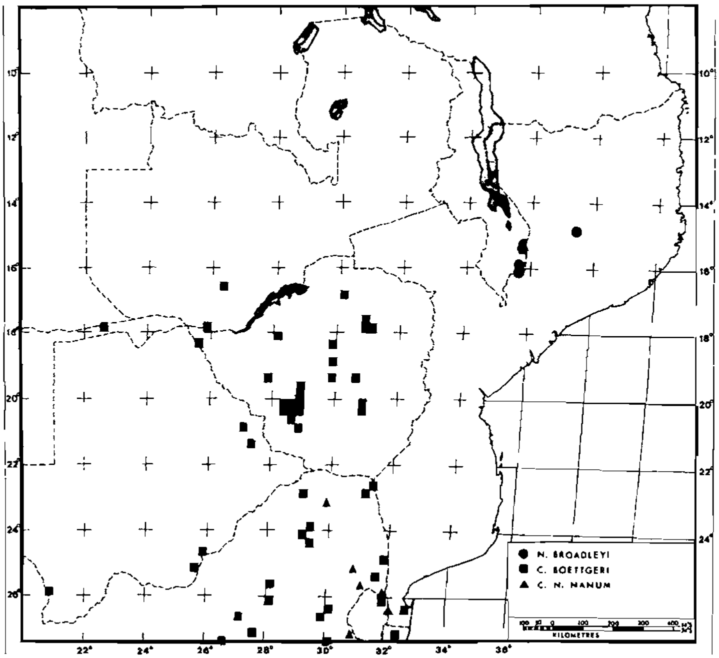
Map 31. *Phrynobatrachus natalensis*.



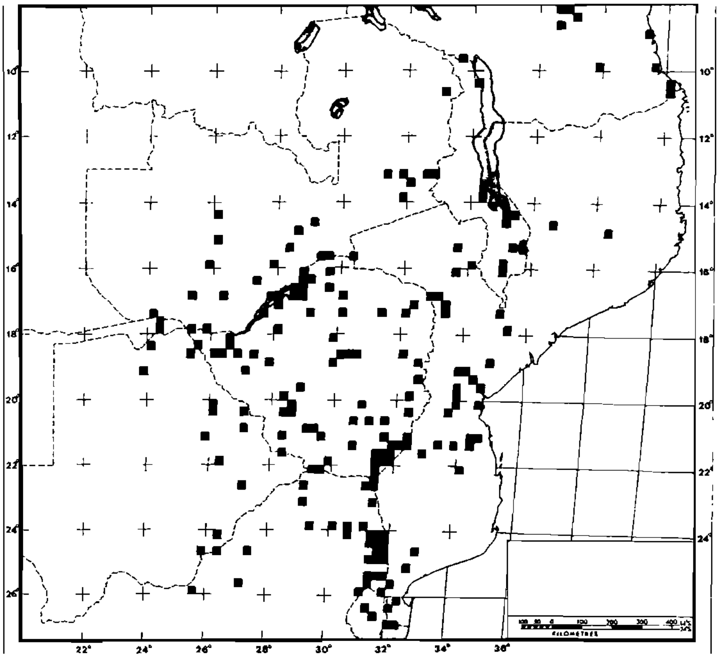
Map 32. *Phrynobatrachus stewartae*, *P. rungwensis*.



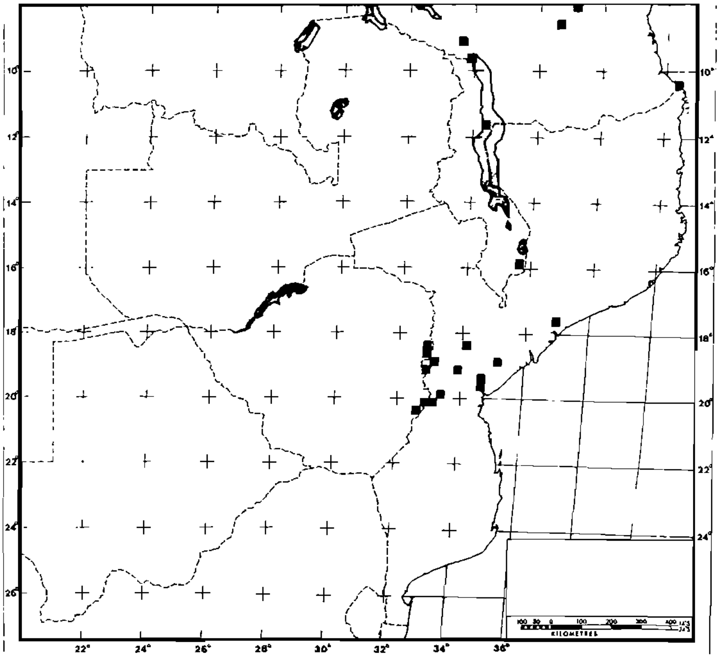
Map 33. *Phrynobatrachus mababiensis, P. parvulus, P. ukingensis.*



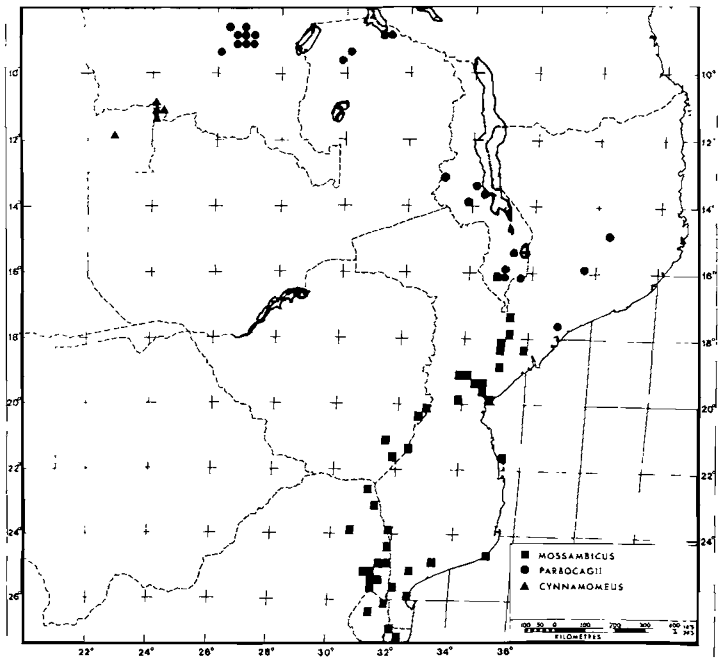
Map 34. *Nothophryne broadleyi, Cacosternum boettgeri, C. n. nanum.*



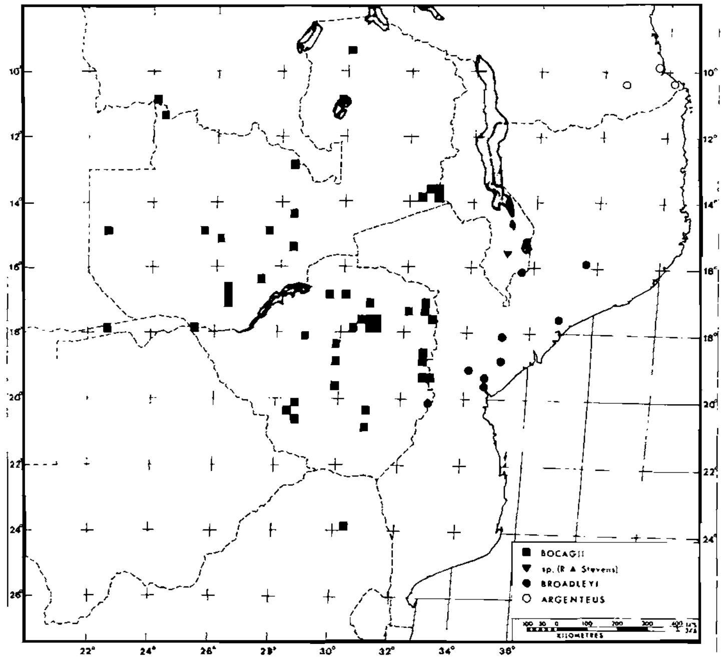
Map 35. *Chiromantis xerampelina.*



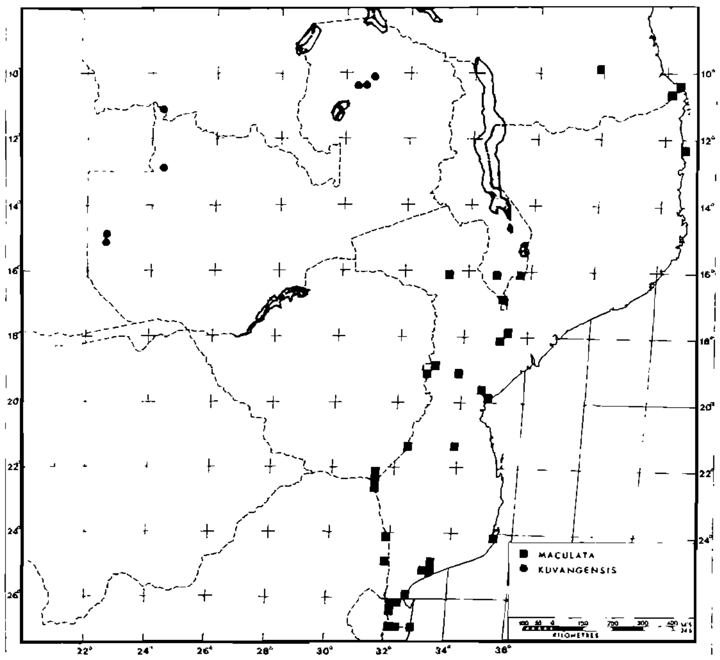
Map 36. *Leptopelis flavomaculatus.*



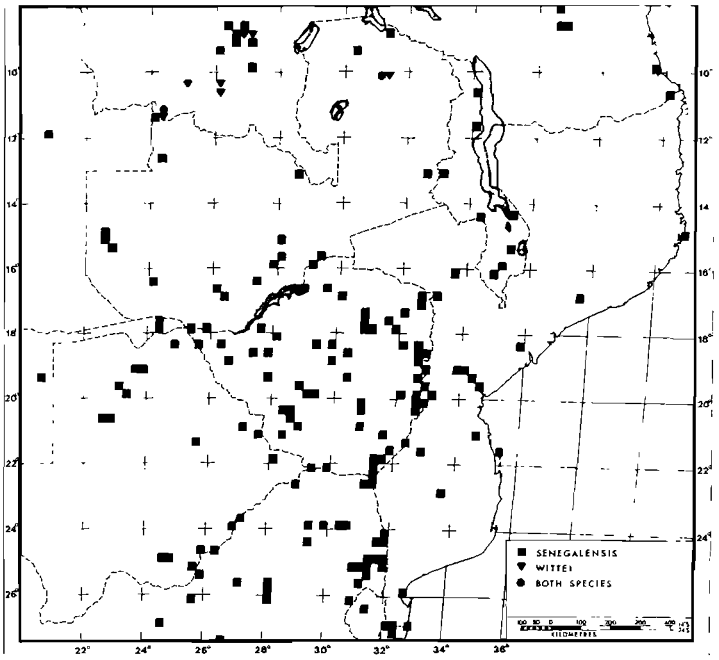
Map 37. *Leptopelis mossambicus, L. parbocagii, L. cynnamomeus.*



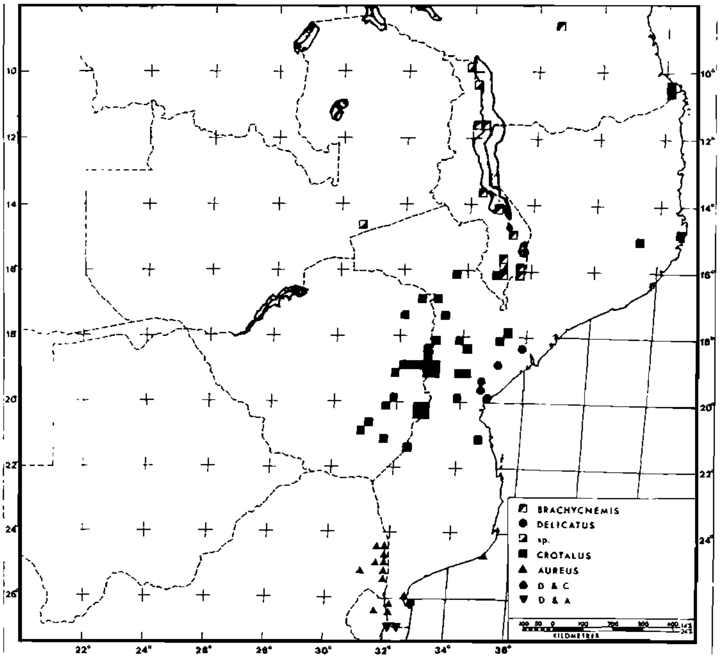
Map 38. *Leptopelis bocagii, L.* sp., *L. broadleyi, (L. argenteus).*



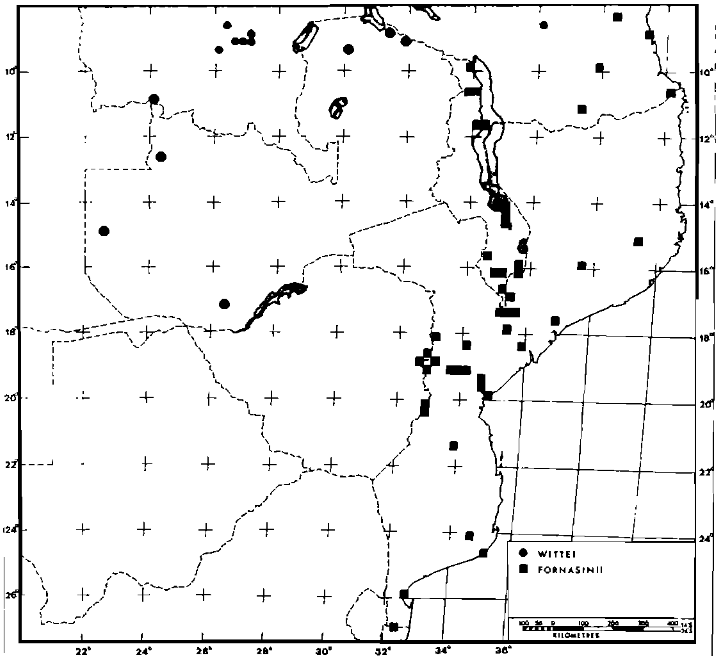
Map 39. *Kassina maculata*, *K. kuvangensis*.



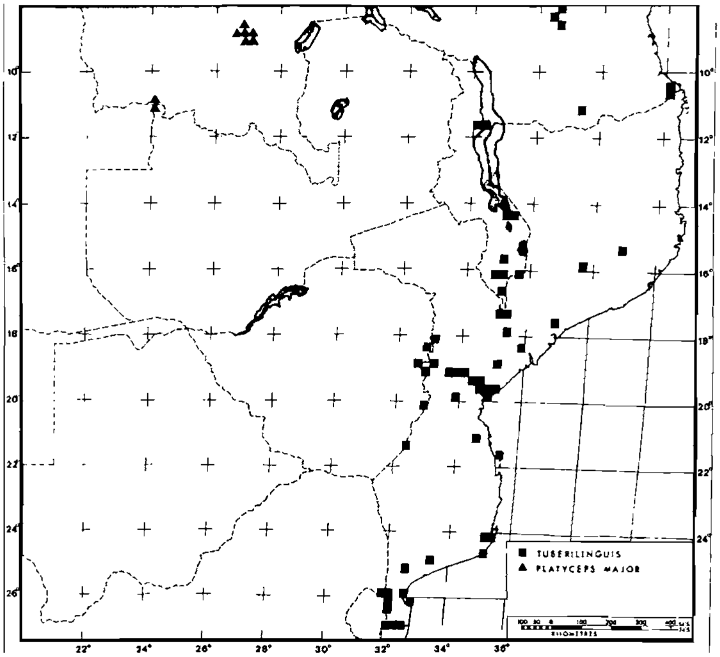
Map 40. *Kassina senegalensis*, *Kassinula wittei*.



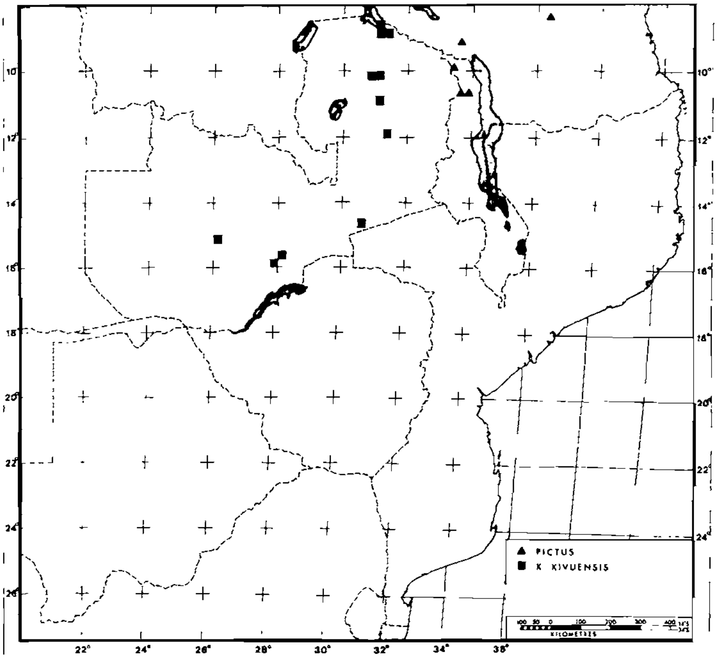
Map 41. *Afrixalus brachycnemis*, *A. delicatus*, *A.* sp., *A. crotalus*, *A. aureus*.



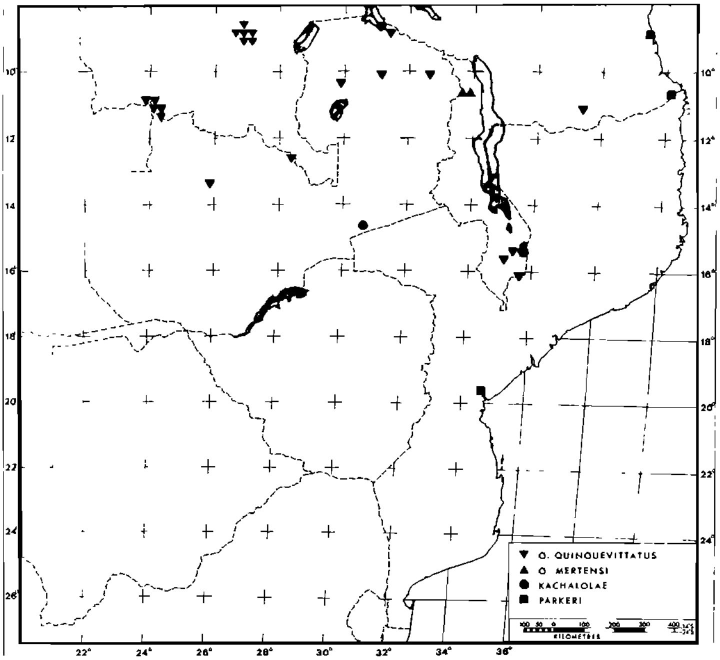
Map 42. *Afrixalus wittei*, *A. fornasinii*.



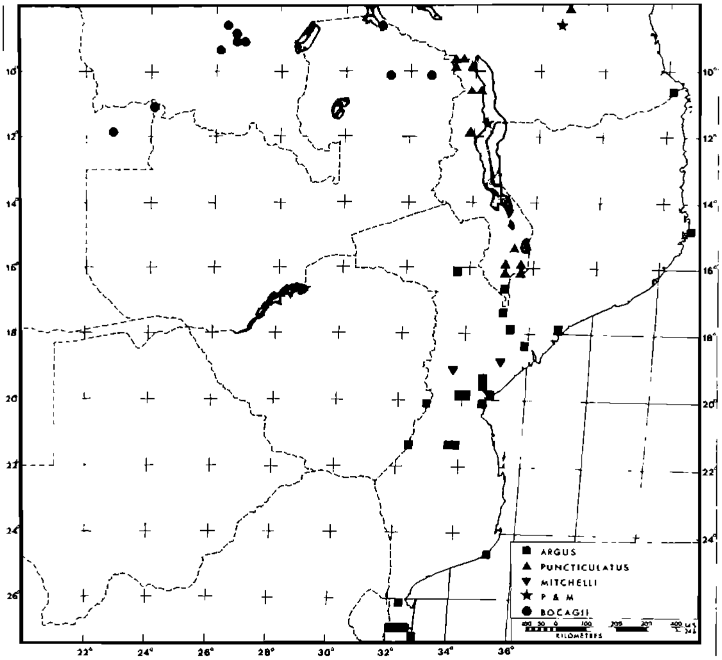
Map 43. *Hyperolius tuberilinguis*, *H. platyceps major.*



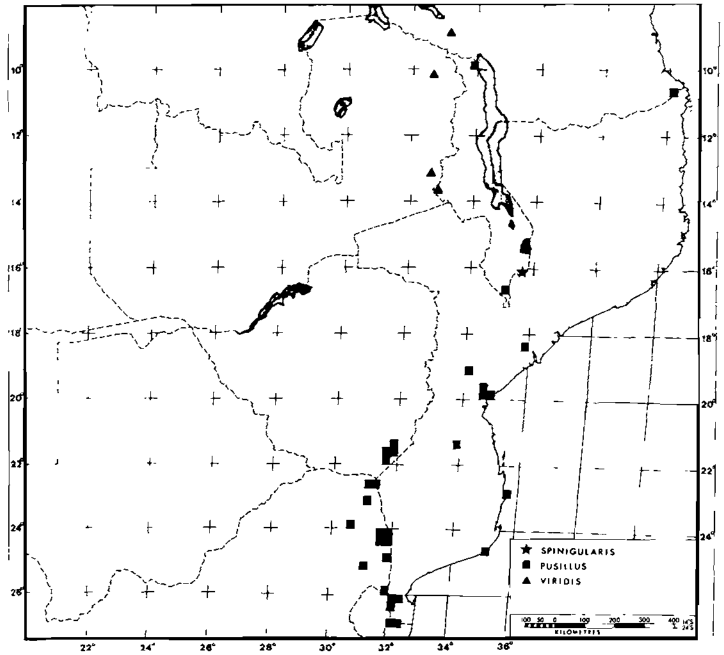
Map 44. *Hyperolius pictus*, *H. k. kivuensis.*



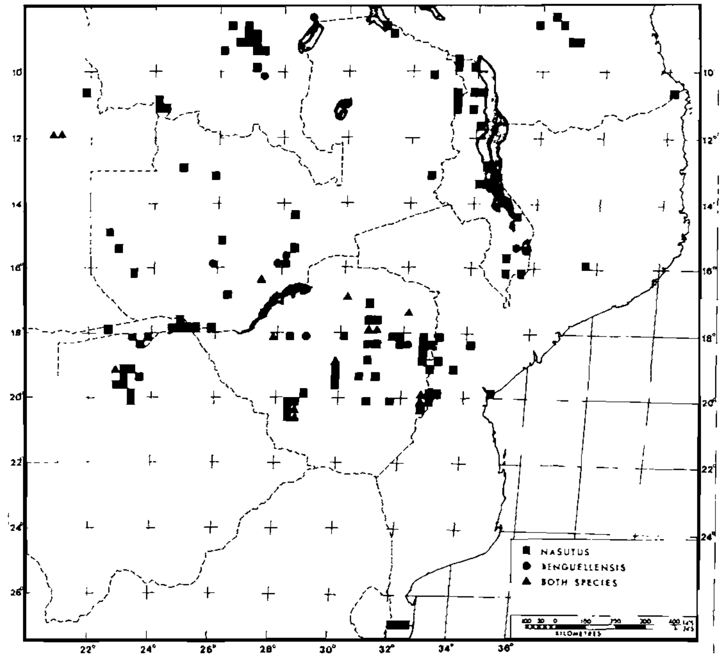
Map 45. *Hyperolius q. quinquevittatus*, *H. q. mertensi*, *H. kachalolae*, *H. parkeri*.



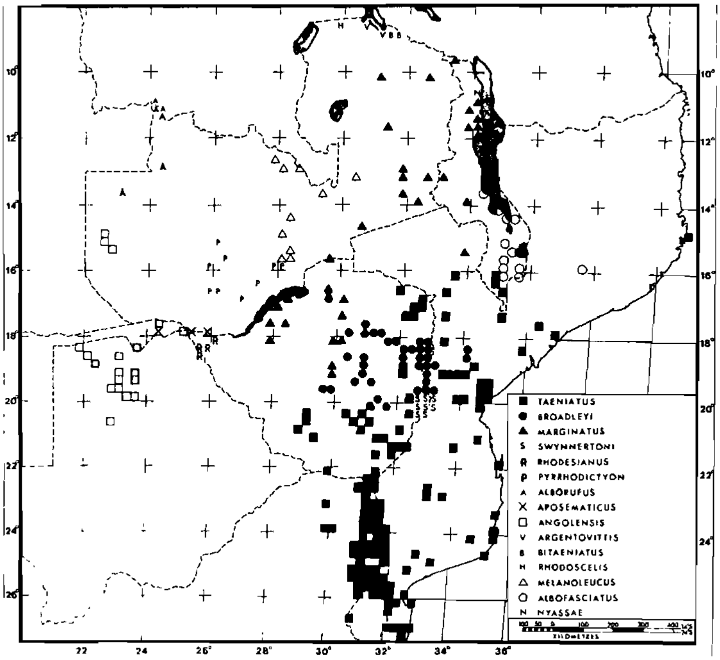
Map 46. *Hyperolius argus*, *H. puncticulatus*, *H. mitchelli*, *H. bocagei*.



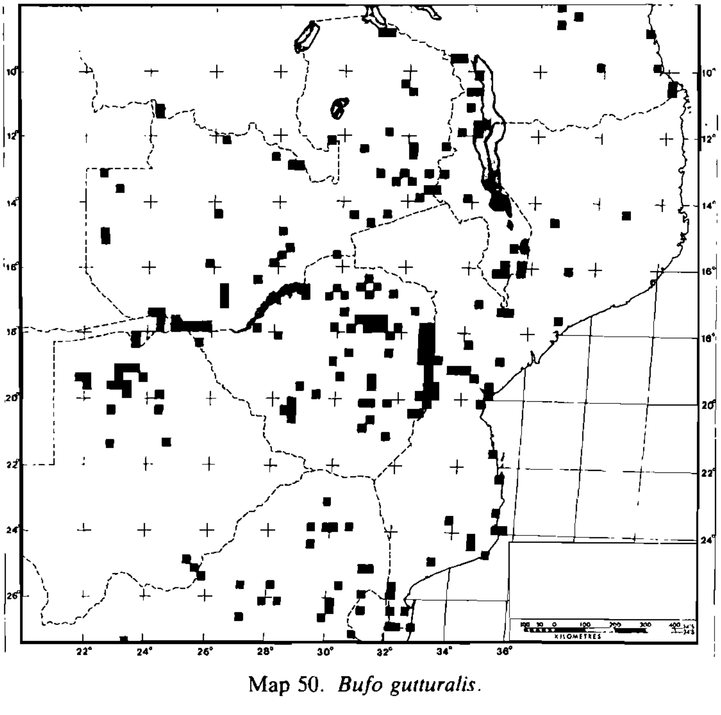
Map 47. *Hyperolius spinigularis*, *H. pusillus*, *H. viridis*.



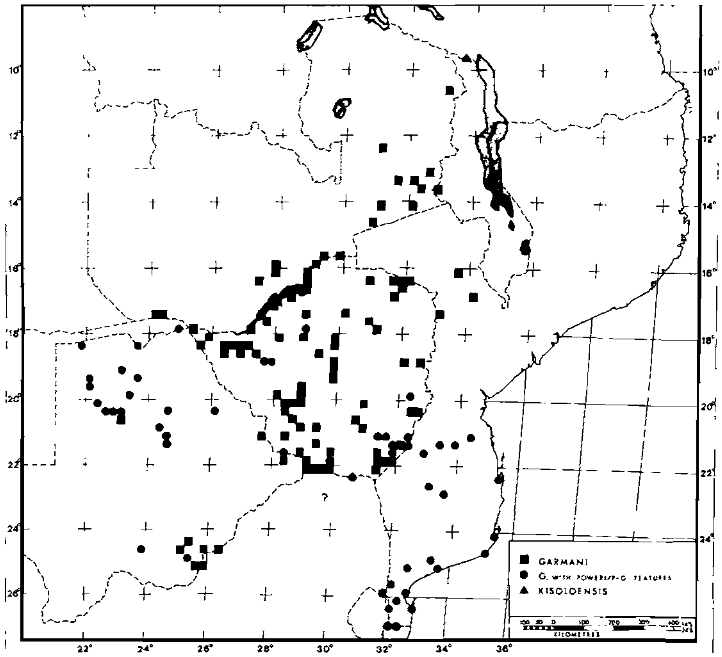
Map 48. *Hyperolius nasutus*, *H. benguellensis*.



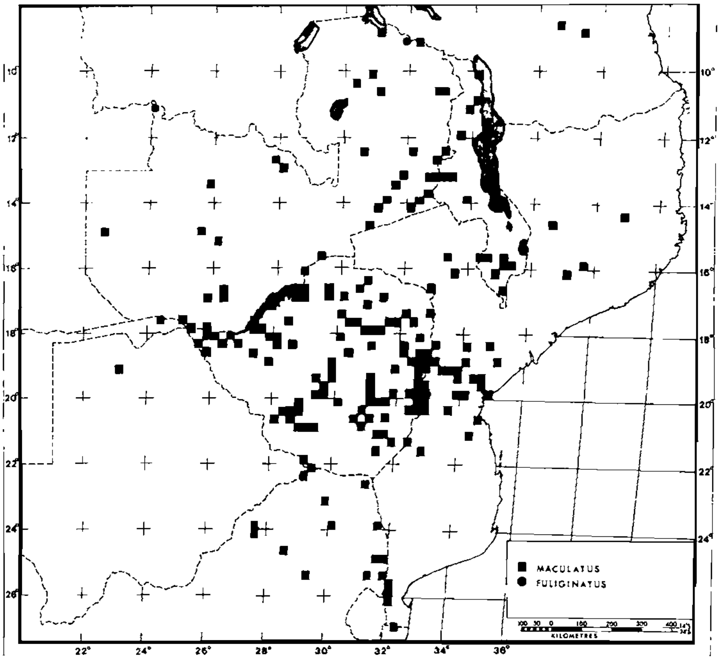
Map 49. *Hyperolius marmoratus taeniatus*, *H. m. broadleyi*, *H. m. marginatus*, *H. m. swynnertoni*, *H. m. rhodesianus*, *H. m. pyrrhodictyon*, *H. m. alborufus*, *H. m. aposematicus*, *H. m. angolensis*, *H. m. argentovittis*, *H. m. bitaeniatus*, *H. m. rhodoscelis*, *H. m. melanoleucus*, *H. m. albofasciatus*, *H. m. nyassae*.



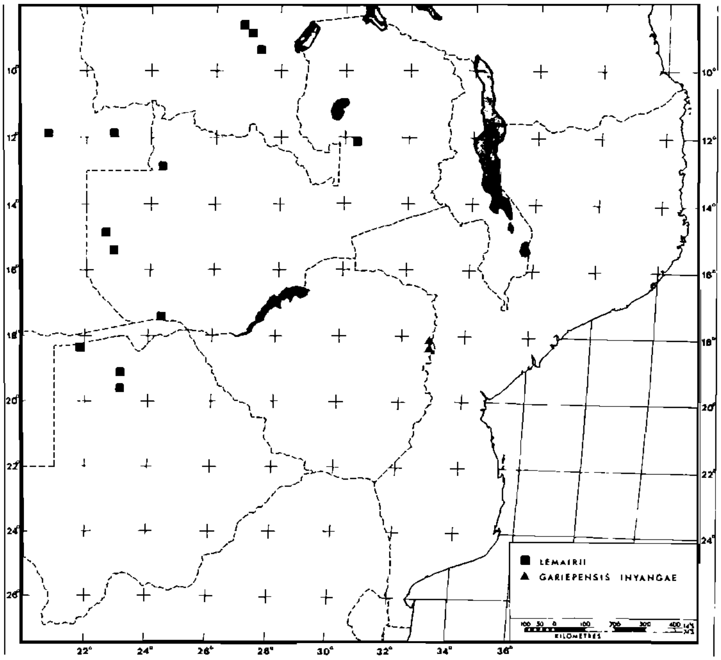
Map 50. *Bufo gutturalis*.



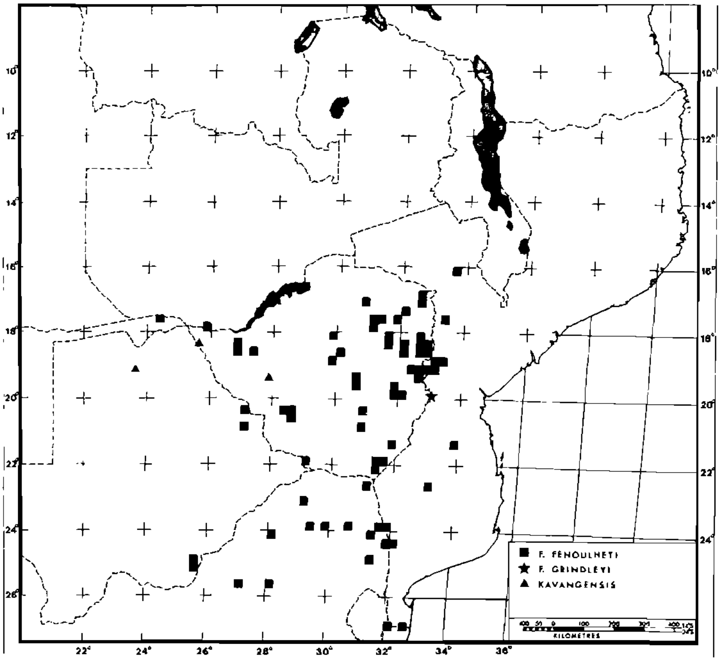
Map 51. *Bufo garmani* (quarter-degree squares are distinguished where specimens have been collected showing any *B. poweri/pseudogarmani* features), *B. kisoloensis*.



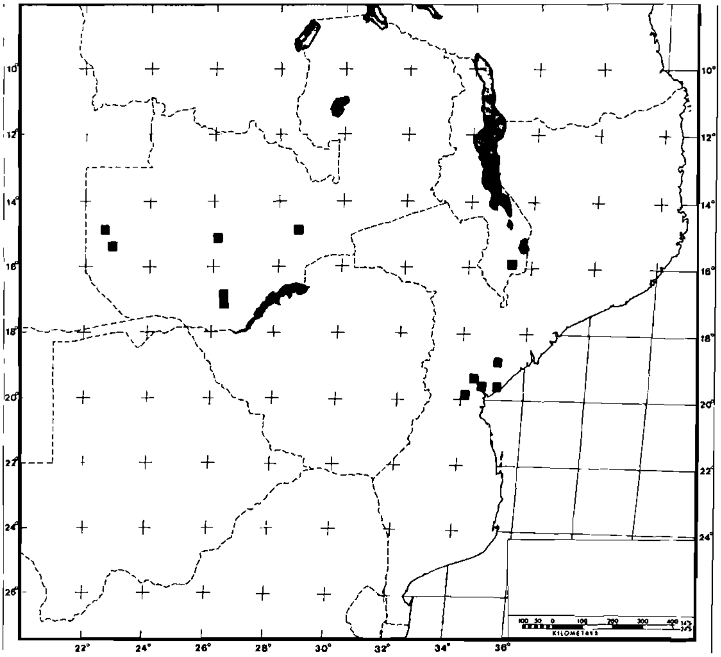
Map 52. *Bufo maculatus*, *B. fuliginatus*.



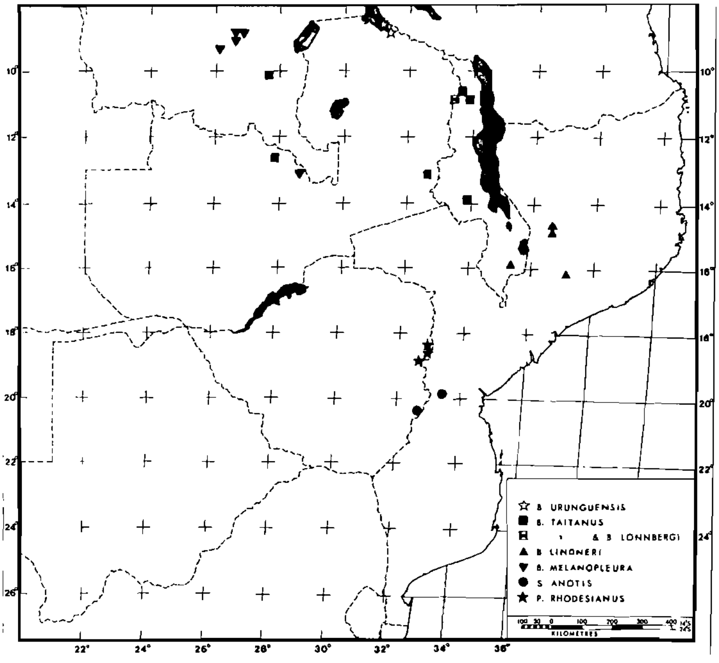
Map 53. *Bufo lemairii*, *B. gariepensis inyangae*.



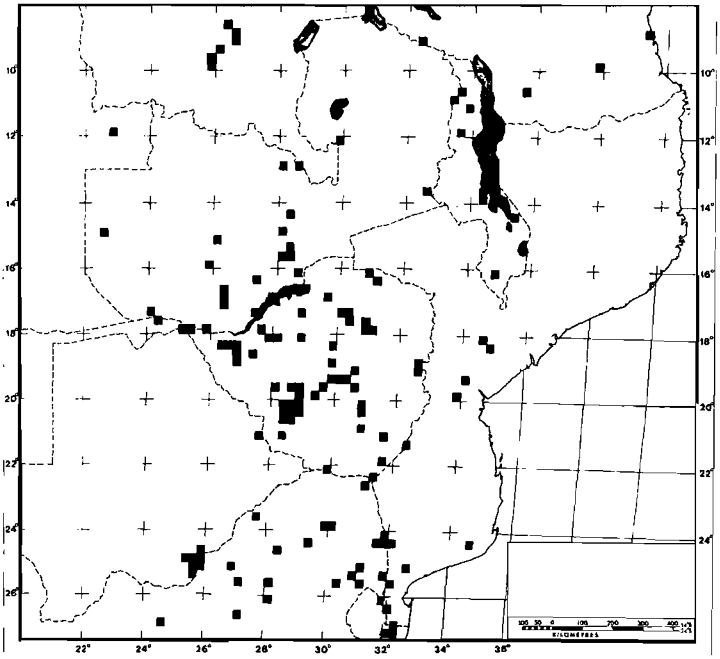
Map 54. *Bufo f. fenouheti*, *B. f. grindleyi*, *B. kavangensis*.



Map 55. *Bufo beiranus*.



Map 56. *Bufo urunguensis*, *B. taitanus*, *B. lonnbergi*, *B. lindneri*, *B. melanopleura*, *Stephopaedes anotis*, *Probreviceps rhodesianus*.



Map 57. *Schismaderma carens.*

LIST OF ZAMBESIACA AMPHIBIANS, GIVING ZOOGEOGRAPHICAL CODING

Note. A full alphabetical index to taxonomic names is given at the end of Part 4 of this series (Poynton & Broadley 1988). The map numbers and page references to main entries are included in this list, giving the part and page number.

C—central, EA—East African lowland, EZ—Eastern Zimbabwe (+ adjacent Mozambique highland), MZ—Malaŵi-Eastern Zambia (+ adjacent Mozambique highland), NC—north-central, NW—northwestern, S—southern.

	Code	Map	Page
Afrixalus aureus	S	41	3:191
Afrixalus brachycnemis	MZ	41	3:187
Afrixalus crotalus	EA	41	3:190
Afrixalus delicatus	?EA	41	3:188
Afrixalus fornasinii	EA	42	3:192
Afrixalus sp.	MZ	41	3:189
Afrixalus wittei	NW	42	3:191
Arthroleptis francei	MZ	9	1:538
Arthroleptis reichei	MZ	9	1:539
Arthroleptis stenodactylus	EA	8	1:536
Arthroleptis troglodytes	EZ	9	1:539
Arthroleptis xenochirus	NW	10	1:540
Arthroleptis xenodactyloides	MZ	10	1:542

	Code	Map	Page
Breviceps a. adspersus	C	5	1:523
Breviceps mossambicus	EA	5	1:517
Breviceps poweri	NC	5	1:525
Bufo beiranus	C	55	4:476
Bufo f. fenoulheti	C	54	4:466
Bufo f. grindleyi	EZ	54	4:471
Bufo fuliginatus	NC	52	4:463
Bufo gariepensis inyangae	EZ	53	4:464
Bufo garmani	EA	51	4:455
Bufo gutturalis	EA	50	4:452
Bufo kavangensis	C	54	4:472
Bufo kisoloensis	MZ	51	4:459
Bufo lemairii	NW	53	4:464
Bufo lindneri	?EA	56	4:480
Bufo lonnbergi	MZ	56	4:479
Bufo maculatus	EA	52	4:460
Bufo melanopleura	NC	56	4:481
Bufo taitanus	NC	56	4:478
Bufo urunguensis	NC	56	4:477
Cacosternum boettgeri	S	34	2:174
Cacosternum n. nanum	S	34	2:174
Chiromantis xerampelina	EA	35	3:165
Euphlyctis occipitalis	NC	11	2:125
Hemisus guineensis microps	NW	7	1:533
Hemisus guineensis broadleyi	C	7	1:532
Hemisus m. marmoratus	EA	6	1:529
Hemisus wittei	NC	6	1:535
Hildebrandtia o. ornata	EA	19	2:141
Hylarana darlingi	NW	18	2:139
Hylarana galamensis	EA	18	2:140
Hylarana lemairei	NW	18	2:140
Hyperolius argus	EA	46	3:199
Hyperolius benguellensis	NW	48	3:208
Hyperolius bocagei	NW	46	3:212
Hyperolius k. kivuensis	NC	44	3:196
Hyperolius kachalolae	C	45	3:199
Hyperolius marmoratus albofasciatus	MZ	49	3:226
Hyperolius marmoratus alborufus	NW	49	3:221
Hyperolius marmoratus angolensis	NW	49	3:222
Hyperolius marmoratus aposematicus	C	49	3:221
Hyperolius marmoratus argentovittis	NC	49	3:223
Hyperolius marmoratus bitaeniatus	NC	49	3:224

	Code	Map	Page
Hyperolius marmoratus broadleyi	C	49	3:216
Hyperolius marmoratus marginatus	C	49	3:218
Hyperolius marmoratus melanoleucus	C	49	3:225
Hyperolius marmoratus nyassae	MZ	49	3:226
Hyperolius marmoratus pyrrhodictyon	C	49	3:220
Hyperolius marmoratus rhodesianus	C	49	3:220
Hyperolius marmoratus rhodoscelis	NC	49	3:224
Hyperolius marmoratus swynnertoni	EZ	49	3:219
Hyperolius marmoratus taeniatus	EA	49	3:214
Hyperolius mitchelli	EA	46	3:203
Hyperolius nasutus	EA	48	3:206
Hyperolius parkeri	EA	45	3:211
Hyperolius pictus	MZ	44	3:195
Hyperolius platyceps major	NW	43	3:195
Hyperolius puncticulatus	MZ	46	3:210
Hyperolius pusillus	EA	47	3:205
Hyperolius q. mertensi	MZ	45	3:198
Hyperolius q. quinquevittatus	NW	45	3:197
Hyperolius spinigularis	MZ	47	3:204
Hyperolius tuberilinguis	EA	43	3:194
Hyperolius viridis	MZ	47	3:206
Kassina kuvangensis	NW	39	3:179
Kassina maculata	EA	39	3:178
Kassina senegalensis	EA	40	3:180
Kassinula wittei	NC	40	3:184
Leptopelis bocagii	NW	38	3:174
Leptopelis broadleyi	EA	38	3:176
Leptopelis cynnamomeus	NW	37	3:177
Leptopelis flavomaculatus	EA	36	3:168
Leptopelis mossambicus	EA	37	3:169
Leptopelis parbocagii	NW	37	3:171
Leptopelis sp.	MZ	38	3:175
Nothophryne broadleyi	MZ	34	2:173
Phrynobatrachus acridoides	EA	30	2:158
Phrynobatrachus mababiensis	EA	33	2:165
Phrynobatrachus natalensis	?NW	31	2:160
Phrynobatrachus parvulus	NW	33	2:169
Phrynobatrachus perpalmatus	NC	30	2:158
Phrynobatrachus rungwensis	NC	32	2:164
Phrynobatrachus stewartae	MZ	32	2:163
Phrynobatrachus ukingensis	MZ	33	2:171
Phrynomerus affinis	NW	4	1:514
Phrynomerus b. bifasciatus	EA	4	1:513

	Code	Map	Page
Probreviceps rhodesianus	EZ	56	1:516
Ptychadena anchietae	EA	21	2:145
Ptychadena ansorgii	NW	25	2:152
Ptychadena broadleyi	MZ	25	2:151
Ptychadena bunoderma	NW	26	2:152
Ptychadena grandisonae	NW	24	2:150
Ptychadena guibei	?EA	27	2:154
Ptychadena keilingi	NW	27	2:154
Ptychadena m. mascareniensis	EA	22	2:148
Ptychadena mossambica	EA	28	2:155
Ptychadena obscura	NC	21	2:147
Ptychadena oxyrhynchus	EA	20	2:144
Ptychadena porosissima	NW	23	2:149
Ptychadena schillukorum	EA	29	2:157
Ptychadena subpunctata	NW	20	2:143
Ptychadena taenioscelis	NW	26	2:153
Ptychadena upembae	NW	24	2:150
Ptychadena uzungwensis	NW	25	2:151
Pyxicephalus adspersus adspersus	S	11	2:122
Pyxicephalus adspersus angusticeps	EA	11	2:123
Pyxicephalus adspersus edulis	EA	11	2:123
Rana angolensis	?NW	15	2:132
Rana j. inyangae	EZ	15	2:135
Rana j. johnstoni	MZ	15	2:134
Schismaderma carens	?EA	57	4:484
Scolecomorphus kirkii	MZ	2	1:506
Stephopaedes anotis	EZ	56	4:483
Strongylopus fasciatus fasciatus	S	17	2:138
Strongylopus fasciatus fuelleborni	MZ	17	2:138
Strongylopus grayii rhodesianus	EZ	16	2:136
Tomopterna cryptotis	?NW	12	2:125
Tomopterna krugerensis	?EA	13	2:127
Tomopterna marmorata	C	14	2:129
Tomopterna natalensis	S	14	2:131
Tomopterna tuberculosa	NW	14	2:130
Xenopus laevis laevis	S	3	1:507
Xenopus laevis petersii	NW	3	1:508
Xenopus muelleri	EA	2	1:511